ECOLOGY

Vol. 36 JANUARY, 1955 No. 1

VARIATIONS IN THE NUMBER OF FIN RAYS OF TWO CYPRINID FISHES CORRELATED WITH NATURAL WATER TEMPERATURES

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Many meristic characters of fish, so important in the definition and description of species and subspecies, are altered by environmental conditions. This view is supported both by observation in nature (Hubbs, 1921 to 1934; Schultz 1927; Schmidt 1917 to 1930) and experimentally (Schmidt 1919a, 1920; Mottley 1931; Heuts 1949). Recent papers by Tåning (1952) and Lindsey (1954) present the most complete experimental proof.

Undoubtedly the allowable limits for the expression of such characters are determined by heredity, and Schmidt has shown that some fine "racial" distinctions are inherited. On the other hand, through changes in environmental conditions it is possible to so alter characters as to produce non-inherited phenocopies of known genotypes (Tåning 1952; see also Child, 1942, for *Drosophila*). Experimentalists have demonstrated that environment is effective particularly during certain phenocritical periods, especially before hatching. Furthermore, factors that affect the metabolic rate, such as temperature and oxygen supply, seem to be the most determinative.

The range in variability for most meristic characters of fish is small, making them difficult to analyze. *Richardsonius balteatus,* a common cyprinid in the Columbia River drainage, is exceptional in the wide range of its anal fin ray numbers, and in this respect attracted the attention of Eigenmann (1895a, 1895b), Gilbert and Evermann (1895), Snyder (1907) and Lindsey (1953). Eigenmann developed a relation between the average anal ray numbers and the elevation at which the fish were collected. He reported that fish from lower altitudes had more rays than those from higher altitudes. Lindsey found the mean numbers of anal rays to be be greater in warm water than in cool water and an indication that more rays are produced towards northern latitudes. Some of the results of these two investigators are in opposition to my findings and will be compared later.

In western Montana the anal rays of *Richardsonius balteatus balteatus* vary from 12 to 18 in number. Also this redside shiner is abundant in warm springs as well as in much colder streams and lakes. These circumstances led to investigating whether or not there existed within a limited geographic area a correction between water temperature and the number of the shiner's dorsal and anal rays.

Another cyprinid, *Ptychocheilus oregonense* was collected from the same stations as the shiners and counts were made of their dorsal and anal rays. This served as a check, for if this species' fin rays were influenced in the same direction as the shiners', environmental induction would seem more probable than genetic differences.

METHODS AND COLLECTION STATIONS

Squawfish (*Ptychocheilus*) and shiners were obtained with seines. All fish in the hauls were included in the counts except the very small specimens that could not be accurately reckoned and a few that had malformed fins. The rays were fully developed in all. Counts were according to the procedure suggested by Hubbs and Lagler (1947). Inasmuch as males and females displayed no significant difference in numbers of fin rays, the sexes were not treated separately. However, Lindsey (1953) reported a sexual difference in some of his collections.

Collections were taken from two warm springs. One near Bearmouth, Montana, has a temperature that remains 24° C in spring and early summer. Unfortunately, this spring was converted into a swimming pool shortly after our first seining, destroying it as a further source of specimens. The second warm spring, called Shandy's Slough, is several miles east of Bearmouth. The only place in this slough where shiners and squawfish spawn is in gravel around its welling spring holes (Weisel and Newman 1951). The rest of the slough has a deep mud bottom. The water

[1] Dr. Ludwig G. Browman and Dr. Royal B. Brunson kindly aided in the collection of temperature data.

temperature in the springs proper is a constant 17.5° C and is the temperature at which the developing eggs and prolarvae are subjected. Both warm springs debouch almost directly into the Clarkfork River and allow free passage to fish.

As to the other places where collections were taken, both Union Creek and Frenchtown Ditch are used for irrigation. They are quite warm as their flow is slow and part of their water seeps back after standing on fields. The Clearwater River is also warm for this area. It passes through a series of medium-sized lakes. Elbow Lake is the last in the chain. The Bitterroot River is colder. It is fed by numerous streams falling directly from the Bitterroot Range. Post Creek originates in the rugged Mission Range and is rather cold. Holland Lake is a medium-sized mountain lake fed from the mountains, but it warms in summer months. Flathead Lake is large, about 210 square miles in area, and except in the shallow Polson Bay, remains cold throughout the year.

None of the waters included in this study are physically isolated. They are all a part of the Clarkfork drainage and overland are within a 75-mile circle. They are well aerated. Even the warm springs at Shandy's Slough contained 9 ppm. of oxygen. The altitudes *per se* are probably not an important factor. Holland Lake is highest at 4100 ft. and the Post Creek station lowest at 2900 ft.

It is impossible to determine exactly what the temperature of the lakes and streams is when it impinges on the critical stages of the developing fish. Not only are there marked weekly changes, but there is often a range of several degrees from morning to evening, and in Yellow Bay of Flathead Lake quiet pockets along the shore were as much as 8.5° C warmer than the center of the bay. However, to obtain a general comparison of the various waters, their temperatures were recorded (close to where the fish were netted) between 11 AM and 3 PM almost every weekend from the middle of April to the last of July. These months include the season when the two cyprinids spawn. Admittedly, the relative temperatures are thus only roughly compared, but it can be stated with assurance that the two springs and Union Creek have exceptionally warm water for this area, that Flathead Lake is consistently cold, and that the other stations are intermediate (Tables I and III).

Chi-square and maximum likelihood tests were applied by the Statistics Laboratory, Montana State University, to examine whether the hypothesis was valid that the distribution of ray counts was the same for all locations. These tests were used on other data as well and the values of chi-square and its 1 percent critical level are presented below each table.

TABLE I. *Anal fin ray counts of* Richardsonius balteatus *from various localities*

Place and year collected	Range and average water temperature °C	Number specimens	Anal rays							Average of anal rays
			12	13	14	15	16	17	18	
Bearmouth, 1949	24.0	31	—	9	20	2	—	—	—	13.77
Shandy's, 1950	17.5	207	1	21	70	91	23	1	—	14.56
Shandy's, 1952	17.5	206	—	7	78	80	35	6	—	14.78
Union Creek, 1949	(10.0-24.5) 15.9	16	—	3	4	5	4	—	—	14.62
Frenchtown Ditch, 1951	(10.0-19.0) 15.0	106	—	4	37	35	27	3	—	14.88
Post Creek, 1950	(10.0-20.0) 13.2	204	—	1	15	68	84	33	3	15.69
Clearwater River, 1949	(7.0-21.0) 12.7	40	—	—	9	14	17	—	—	15.20
Holland Lake, 1949	(7.0-21.0) 11.5	19	—	—	—	9	5	4	1	15.84
Clarkfork River, 1949	(7.5-18.0) 11.4	63	—	3	15	28	13	4	—	15.00
Flathead Lake, 1950	(6.0-15.5) 8.3	51	—	—	—	12	24	13	2	16.09
Total		943	Grand Average							15.04

$\chi^2 = 134.2$; the 1% critical level is 50.0.

RESULTS

The average number of anal rays of the shiner is moderately well correlated with water temperature (Table I). Fish from the warmer habitats have lower counts than those from colder waters. There is a statistically significant difference with location. However, the collection from Union Creek is intermediate between those from Shandy's Slough in 1950 and 1952. The Union Creek averages are based on too few specimens to be significant, but the difference between the two collections from Shandy's is remarkable in view of the fact that water temperatures were similar in this warm spring in the two years.

The specimen from Shandy's with only 12 anal rays is a phenocopy of *Richardsonius balteatus hydrophlox,* which occurs in the Snake River of Idaho but not in the Clarkfork drainage.

The dorsal rays of the shiner also differ significantly with location, but they do not relate as well as the anal rays to the temperatures (Table II). There is a marked displacement in the case of collections from Holland Lake and Clearwater River.

The fin rays of squawfish vary in number much less than those of the redside shiner. There are only 8 or 9 in the anal, and 8, 9, or 10 in the dorsal. The anal rays are consistently 8 except for one fish from the Clearwater and six from

TABLE II. *Dorsal fin ray counts of* Richardsonius balteatus *from various localities*

Place and year collected	Range and average water temperature °C	Number specimens	Dorsal rays				Average of dorsal rays
			8	9	10	11	
Bearmouth, 1949	24.0	31	—	6	24	1	9.83
Shandy's, 1950	17.5	207	1	31	171	4	9.86
Shandy's, 1952	17.5	206	—	31	167	8	9.88
Union Creek, 1949	(10.0-24.5) 15.9	16	—	4	12	—	9.75
Frenchtown Ditch, 1951	(10.0-19.0) 15.0	106	—	8	94	4	9.96
Post Creek, 1950	(10.0-20.0) 13.2	204	—	9	171	24	10.07
Clearwater River, 1949	(7.0-21.0) 12.7	40	—	7	33	—	9.82
Holland Lake, 1949	(7.0-21.0) 11.5	19	—	6	13	—	9.68
Clarkfork River, 1949	(7.5-18.0) 11.4	63	—	5	54	4	9.98
Flathead Lake, 1950	(6.0-15.5) 8.3	51	—	—	42	9	10.17
Total		943	Grand Average				9.90

χ^2=356.0; the 1% critical level is 105.4.

TABLE IV. *Dorsal fin ray counts of* Ptychocheilus oregonense *from various localities*

Place and year collected	Range and average water temperature °C	Number specimens	Dorsal rays			Average of dorsal rays
			8	9	10	
Shandy's, 1950	17.5	151	17	134	—	8.88
Shandy's, 1952	17.5	103	3	100	—	8.97
Frenchtown Ditch, 1951	(10.0-19.0) 15.0	57	1	56	—	8.98
Elbow Lake, 1950	(7.0-21.0) 12.7	14	—	13	1	9.07
Clearwater River, 1949	(7.0-21.0) 12.7	51	—	50	1	9.02
Bitterroot River, 1949	(9.5-19.0) 12.0	35	—	35	—	9.00
Holland Lake, 1949	(7.0-21.0) 11.5	23	—	23	—	9.00
Clarkfork River, 1949	(7.5-18.0) 11.4	2	—	2	—	9.00
Flathead Lake, 1949	(6.0-15.5) 8.3	13	—	12	1	9.07
Flathead Lake, 1951	(6.0-15.5) 8.3	28	—	24	4	9.14
Total		477	Grand Average			9.01

χ^2=69.4; the 1% critical level is 34.8.

Flathead Lake (Table III). The collection from the latter, the coldest water, has significantly more rays.

The squawfish's dorsal rays present a better example of the relationship between ray averages and water temperature (Table IV). The number of rays in fish from warm localities is significantly lower than in those from the cool Flathead Lake.

If the localities are arranged according to the average number of fin rays of fish of the two species taken from each, a similarity in locality sequence is evident (Table V). The anal of the squawfish is of little importance in this collation since the ray counts for all but the last two localities are the same. The averages of dorsal rays of the shiners from Holland Lake and the Clearwater considerably upset what would be an orderly arrangement. Otherwise the warm waters have the low averages and the cold waters the high averages. It is notable that the averages for both species are lower for Shandy's Slough in 1950 than in 1952.

There is a definite tendency in both cyprinids toward a positive correlation between the number of anal rays and the number of their dorsal rays. If there is a low count in one fin, the other is liable to be low, or if high, for the other to be high (Tables VI and VII). The hypothesis that the numbers of anal and dorsal rays are independent was statistically rejected.

TABLE III. *Anal fin ray counts of* Ptychocheilus oregonense *from various localities*

Place and year collected	Range and average water temperature °C	Number specimens	Anal rays		Average of anal rays
			8	9	
Shandy's, 1950	17.5	151	151	—	8.00
Shandy's, 1952	17.5	103	103	—	8.00
Frenchtown Ditch, 1951	(10.0-19.0) 15.0	57	57	—	8.00
Elbow Lake, 1950	(7.0-21.0) 12.7	14	14	—	8.00
Clearwater River, 1949	(7.0-21.0) 12.7	51	50	1	8.02
Bitterroot River 1949	(9.5-19.0) 12.0	35	35	—	8.00
Holland Lake, 1949	(7.0-21.0) 11.5	23	23	—	8.00
Clarkfork River, 1949	(7.5-18.0) 11.4	2	2	—	8.00
Flathead Lake, 1950	(6.0-15.5) 8.3	13	13	—	8.00
Flathead Lake, 1951	(6.0-15.5) 8.3	28	22	6	8.21
Total		477	Grand Average		8.02

χ^2=83.1; the 1% critical level is 21.7.

TABLE V. *Arrangement of localities according to the average of fin ray counts, from low to high*

Dorsal rays		Anal rays	
Richardsonius	*Ptychocheilus*	*Richardsonius*	*Ptychocheilus*
Holland Lake	Shandy's, 1950	Shandy's, 1950	Shandy's, 1950
Clearwater River	Shandy's, 1952	Shandy's, 1952	Shandy's, 1952
Shandy's, 1950	Frenchtown Ditch	Frenchtown Ditch	Frenchtown Ditch
Shandy's, 1952	Clarkfork River	Clarkfork River	Clarkfork River
Frenchtown Ditch	Holland Lake	Clearwater River	Holland Lake
Clarkfork River	Clearwater River	Holland Lake	Clearwater River
Flathead Lake	Flathead Lake	Flathead Lake	Flathead Lake

TABLE VI. *Relation of anal ray counts to dorsal ray counts of* Richardsonius

Dorsal rays	Mean of anal rays	Variance of anal rays	SE of mean
11	15.79	1.23	1.11
10	15.04	0.98	0.99
9	14.57	0.93	0.96

$\chi^2 = 105.1$; the 1% critical level is 34.8.

TABLE VII. *Relation of dorsal ray counts to anal ray counts of* Ptychocheilus

Dorsal rays	Mean of anal rays	Variance of anal rays	SE of mean
9	9.28	0.21	0.46
8	8.96	0.05	0.22

$\chi^2 = 36.27$; the 1% critical level is 9.21.

TABLE VIII. *Anal ray counts of* Richardsonius *of different length groups*

Total length in centimeters was used for the length groups. The length groups range from 3.5-4.4 cm for group 1 to 11.5-12.4 cm for group 9.

Place collected	Size group	Number fish	Mean	SE of mean
Post Creek	1	30	15.50	0.16
	2	68	15.80	0.10
	3	17	15.00	0.24
	4	47	15.89	0.12
	5	27	15.74	0.17
	6	8	15.75	0.42
	7	5	15.20	0.18
	8	1	17.00	0.00
	9	1	16.00	0.00
Clarkfork River	1	1	15.00	0.00
	2	3	13.66	0.27
	3	7	15.28	0.39
	4	39	14.89	0.12
	5	12	15.33	0.32
	6	1	17.00	0.00
Shandy's, 1950	1	22	14.23	0.14
	2	27	14.03	0.18
	3	27	14.55	0.15
	4	53	14.75	0.10
	5	59	14.61	0.12
	6	10	14.90	0.22
	7	6	15.33	0.38
	8	2	15.00	0.00
	9	1	15.00	0.00
Shandy's, 1952	2	48	14.87	0.11
	3	129	14.77	0.08
	4	8	14.87	0.28
	5	13	14.31	0.19
	6	7	15.14	0.24
	7	1	14.00	0.00

χ^2 for Post Creek = 57.2; the 1% critical level is 67.3; the 5% level is 55.4.
χ^2 for Clarkfork River = 44.3; the 1% critical level is 37.6.
χ^2 for Shandy's, 1950 = 70.3; the 1% critical level is 67.3.
χ^2 for Shandy's, 1952 = 75.8; the 1% critical level is 37.6.

Collections of shiners from Shandy's Slough, Post Creek, and Clarkfork River were grouped into 1-cm. length classes and the numbers of anal rays in the classes compared (Table VIII). The lengths chosen for comparison were arbitrary, but they represent fish hatched in different months of a year and fish of different ages. Consequently, each length class probably was subjected to a somewhat different environment during development of its fin rays. There appears to be a significant difference in ray count distribution among length classes since the null hypothesis was rejected. This is true in Shandy's warm springs where the temperature of the water is nearly constant as well as in Post Creek and the Clarkfork where temperatures are quite variable.

SUMMARY AND CONCLUSIONS

In the upper Clarkfork drainage, redside shiners and squawfish from warm habitats tend to have fewer rays in the anal and dorsal fins than those from colder lakes and streams (Fig. 1). These findings are broadly in agreement with those of Hubbs (1922, 1924) and Mottley (1931) on other species of fish.

Furthermore, in a short account, Snyder (1907) listed the number of anal rays of some *Richardsonius* he collected in Oregon from Warm Spring, Silver Creek, and Silvies River. The warm spring and Silver Creek, its outlet, had a constant temperature of 21.1° C whereas the neighboring Silvies was colder. Snyder did not mention any correlation between ray numbers and temperature, but the fish from the warm waters averaged 11 anal rays compared to 14.2 for the river fish.

Although Eigenmann (1895b) and Shultz (1927) found an association between temperatures and fin ray numbers in *Richardsonius balteatus* and *Notemigonus crysoleucas* respectively, the reverse effects were apparent. *Notemigonus* collected from Michigan to Virginia showed a southward increase in anal ray numbers which was attributed to increasing temperatures. Eigenmann's large series of *Richardsonius*, gathered in much the same latitude but from elevations varying from 300 to 5344 ft., exhibited a tendency for a decrease in anal rays from the lower to the higher elevations, or, translated into probable temperatures, a decrease from the warmer to colder temperatures.

Eigenmann made no attempt to compare with temperatures and it is possible that some of his lower altitude stations had colder waters than some of those at higher altitudes. Also, the collections cover a wide geographic range—from Umatilla, Washington, to Brown's Gulch, Mon-

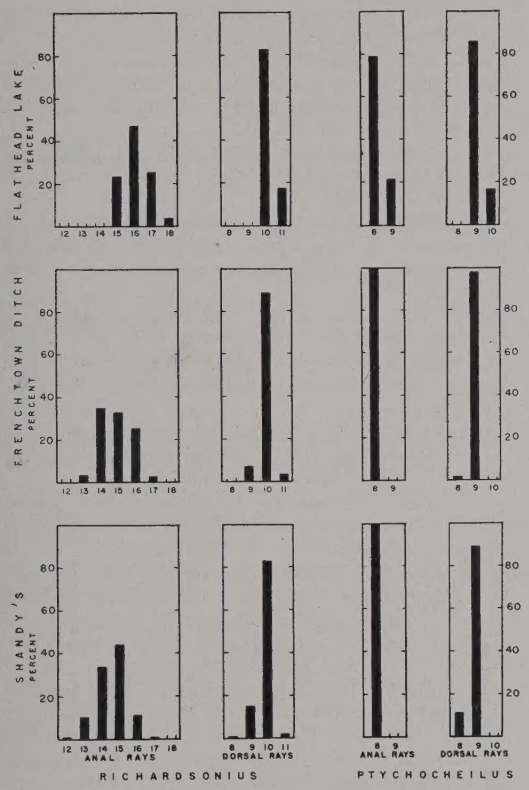

FIG. 1. The frequency of anal and dorsal ray numbers in *Richardsonius balteatus* and *Ptychocheilus oregonense* from warm water (Shandy's), cold water (Flathead Lake), and water of intermediate temperature (Frenchtown Ditch).

tana—which allows the likelihood of his having dealt with different genetic clines.

Gilbert and Evermann (1895) took issue with Eigenmann's findings. Their collections from Lake Washington, Washington, to Brown's Gulch had no difference between the anal ray averages for the lowest and the highest elevations. They could see no reason for the generalization, "the higher the altitude the fewer the number of rays." At the present time there is no further evidence that altitude as such affects the meristic characters of fish.

Lindsey (1953) counted anal fin rays of large series of *Richardsonius balteatus* collected in British Columbia. He found a positive correlation between water temperature and the mean number of anal rays, significant differences in counts between different bodies of water, between recently introduced populations and their parent stock, between different parts of the same lake, and between different year classes. He also made comparisons with recorded ray counts from the United States. These indicated a tendency for higher ray counts towards the north.

Lindsey's results in relating the number of anal rays to water temperatures are directly opposite to mine. Fish from cold waters averaged fewer rays than those from warm waters. At present this contradiction cannot be explained satisfactorily, especially since the water temperatures in both investigations were comparable. However, it does indicate that no simple generalization can be made concerning thermal influence on the meristic characters of fish.

I agree with Lindsey that the increase from south to north of anal rays of *Richardsonius* is probably genetic. This may have occurred by intrusion from the north of *R. b. balteatus* upon *R. egregius*. The present range of *R. egregius* is in northern California and the Lahontan system of Nevada. This species usually has 8 to 9 anal rays. *R. b. balteatus* occurs in the Columbia Basin and the Skeena and Fraser systems of British Columbia, and has 12 to 22 anal rays. *R. b. hydrophlox* represents an intermediate group that may have resulted from contact between the two species. This subspecies occurs in the Bonneville Basin and the Snake River above its falls, and has 10 to 13 anal rays. If this is the case, it is probable that *R. b. balteatus* retains more of the genetic influence of *R. egregius* in its southern range than in its northern range. Also, there may be isolated pockets in the upper reaches of the Columbia system, such as Shandy's Slough, where the fish possess more of the inherited tendency toward fewer rays.

Besides heritable variations, shifts in ray numbers can be caused by such environmental influences as sudden cold snaps or warm spells, changes in oxygen and carbon dioxide concentration, and crowding during the critical period of ray formation. Another condition that may lead to misinterpretation is that meristic characters can have their optimum expression at a certain temperature and undergo a decrease in their numbers at temperatures either above or below it (Schmidt 1919a; Tåning 1952; Lindsey 1954). The possibilities of sexual dimorphism and temporary immigrations of fish from other habitats must be considered as well. Also, there is the fact that most fish tend to spawn within a certain temperature range so that those in colder waters may not reproduce until the water warms to about that of environments where the fish have spawned earlier. This increases the difficulty of choosing the correct times to use for temperature comparisons.

In most field studies of this sort the results are

not so concise as in controlled laboratory experiments. But field studies do have definite advantages. Experimental studies have used temperatures that are not in the natural range of the fish. Feeding, spacing, water flow, etc. also introduce artificial factors.

A number of perplexing results are obvious in this investigation. For instance, the dorsal rays of the shiner do not closely follow the general pattern of that species' anal rays and the rays of the squawfish. There is a marked difference in the ray numbers of fish taken from Shandy's in 1950 as compared to those taken in 1952, although the water temperature was quite constant. There is a significant variation in the anal rays of shiners in different size groups from the warm spring as well as from waters of radically fluctuating temperatures.

However, the contention that natural thermal influence is one of the main factors that causes the number of dorsal and anal fin rays of *Richardsonius* and *Ptychocheilus* to differ with locality is supported by four lines of evidence. (1) Collections were from a limited area with no isolating physical barriers. (2) There is a definite trend for both the anal and the dorsal rays to vary inversely with water temperature. (3) Both the shiner and the squawfish have their fin rays molded in the same direction. (4) Shiners in different size groups, which consequently must have developed at different times under unlike environmental conditions, tend to have significantly different anal ray counts. This is true in single populations and it is difficult to believe that it is due to inherited shifts.

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THE SPECIES—AREA CURVE

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Cain (1938) reviewed thoroughly the various uses made of the species-area curve. Most applications of the curve necessitate the location of the so-called break in the curve (*i.e.*, the point at which the curve flattens strongly). The original practice was to locate the "break" by inspection. Location by this method is very arbitrary and, as pointed out by Cain (1938), depends upon the y-x ratio used in constructing the curve. Cain suggested, therefore, the determination of a point at which the curve has a certain percentile rise. He suggested further that, in terms of his experience, sampling is adequate when a 10 per cent increase in sample area results in a 10 per cent increase in the number of species. Such a point can be easily located mechanically (Cain 1938) on any species-area curve regardless of the ratio of the y and x axes. As Cain (1943) explained later, this point is the point on the curve where the increment in new species is equal to the average value of this increment as determined by dividing the total number of species encountered by the total area sampled. The accuracy with which the 10 per cent point could be located caused many workers to use the above method (Oosting and Billings 1939, Cain 1943, Oosting 1948, Quarterman 1950, Merkle 1951, Livingston 1952, Rice 1952). Cain (1943), however, pointed out that, "the location of such a point . . . on the species-area curve, and its indication of minimal area, depend upon the total area sampled." Moreover, Ashby (1948), Vestal (1949), and Goodall (1952) pointed out the same weakness in the above procedure.

While analyzing a tall-grass prairie in Marshall County, Oklahoma, in the summer of 1952, species-area curves were made on the basis of 20 quadrats and on the basis of 40 quadrats. It was found that the 10 per cent point of Cain increased with each addition in the number of quadrats. Prior to this experience, the warnings of Cain, Ashby, Vestal, and Goodall had escaped the attention of the authors. It was decided, therefore, that a careful restatement of the problem documented with results of field experiments might be of value to persons with little experience in vegetational analysis.

METHODS

A tall-grass prairie plot about one-half acre in extent, located about 8 miles southwest of Norman, Oklahoma, in McClain County, was analyzed by the use of 100 one-tenth square meter quadrats (square) spaced evenly throughout the plot. Species-area curves were then constructed on the basis of different numbers of quadrats (the chosen number being distributed evenly throughout the plot). The 10 per cent point was located mechanically on each curve by the method suggested by Cain (1938). Species-area curves were constructed also from other available data.

RESULTS AND DISCUSSION

The minimal number of quadrats as indicated by the 10 per cent point for the McClain County prairie, shifted as follows: 2.5 based on 10 quadrats; 5 based on 20; 11 based on 40; 16 based on 60; 22 based on 100 (Fig. 1). It should be emphasized here that this shift occurred on different portions of the same curve.

When species-area curves were constructed based on different numbers of quadrats evenly distributed throughout the plot, the 10 per cent point increased as the number of quadrats on which the curve was based increased (Fig. 2). Per cent of species and per cent of quadrats (per cent of sample area) were used, rather than the numbers of each, so that the same y-x ratios could be used in all cases. It is evident that the 10 per cent point is the same regardless of which system is used (e.g., the 10 per cent point based on 100 quadrats was at 22 quadrats in both Figs. 1 and 2). Species-area curves were drawn for all possible sets of 10 quadrats (in geographic order and with uniform spacing), several sets of 20, several of 25, and two of 50; and it was found that the same sort of shift in the 10 per cent point occurred in all cases as the number of quadrats was increased. There were slight variations, of course, in 10 per cent points on the various curves based on 10 quadrats, or the various curves based on 20, etc.; but the differences were not as great as when the 10 per cent points were based on appreciably fewer or more quadrats.

Similar shifts in the 10 per cent point were

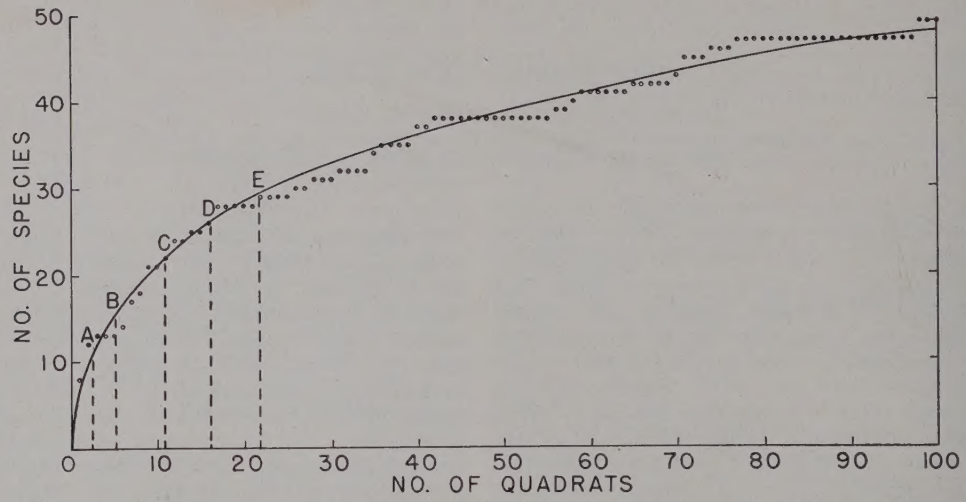

FIG. 1. Species-area curve for the McClain County prairie. The quadrats were added to the curves in systematic geographic order in all figures. The 10 per cent point, as defined by Cain (1938) and determined mechanically, moves to the right when the number of quadrats utilized in its determination is increased: A, based on 10 quadrats; B, 20; C, 40; D, 60; E, 100.

found to occur when species-area curves were drawn for two prairie plots in Marshall County, Oklahoma (Fig. 3) and for the herbaceous species in an evergreen oak forest in the vicinity of New Orleans, La. (Penfound and Howard 1940) (Fig. 4). Although not shown, many curves were drawn for woody species based on data from various published sources, and the minimal number of quadrats indicated by the 10 per cent point always increased as the number of quadrats on which it was based was increased.

From a mathematical standpoint, the shift described above would, of course, be expected. Even if the species-area curve becomes completely horizontal, the point continues to shift to the right as the number of quadrats is increased, and approaches the beginning of the flat portion of the curve as the number of quadrats approaches infinity. This can be understood by recalling that the 10 per cent point is defined as that point on the curve where a 10 per cent increase in the area sampled gives a 10 per cent increase in species. Stated differently, this means that the point desired is that location on the curve at which the slope equals

$$\frac{10\% \text{ of the species.}}{10\% \text{ of the quadrats.}}$$

When the number of quadrats becomes infinite, the above slope becomes

$$\frac{10\% \text{ of the species,}}{\infty}$$

which equals zero, and the first point on the curve at which the slope becomes zero is that point where the curve becomes parallel to the x-axis.

The chief use of the species-area curve in this country has been in indicating minimal quadrat size and minimal numbers of quadrats required for adequate sampling. If the point which one locates to indicate the desired information shifts with a change in the number of quadrats used in locating it, it would seem that such a point has little value as an indicator of adequacy of sampling. Certainly, the location of the "break" in the curve by inspection is questionable because of its inaccuracy in most instances. If a given species-area curve becomes completely horizontal or has a definite "break" which can be located by inspection, the use of such a curve is probably of considerable value in giving the sampler some confidence in his results. This is particularly true if he is interested only in a semi-quantitative description of a given plant community. In actual practice most workers will no doubt continue to take as many quadrats in any given study as their field experience indicates, or their time and funds allow.

If, in a study of a given plant community, one wishes to obtain quantitative results for each characteristic species on cover, density, or frequency that can be reproduced by sampling the same number of different quadrats; it is doubtful that the species-area curve as it has been used commonly

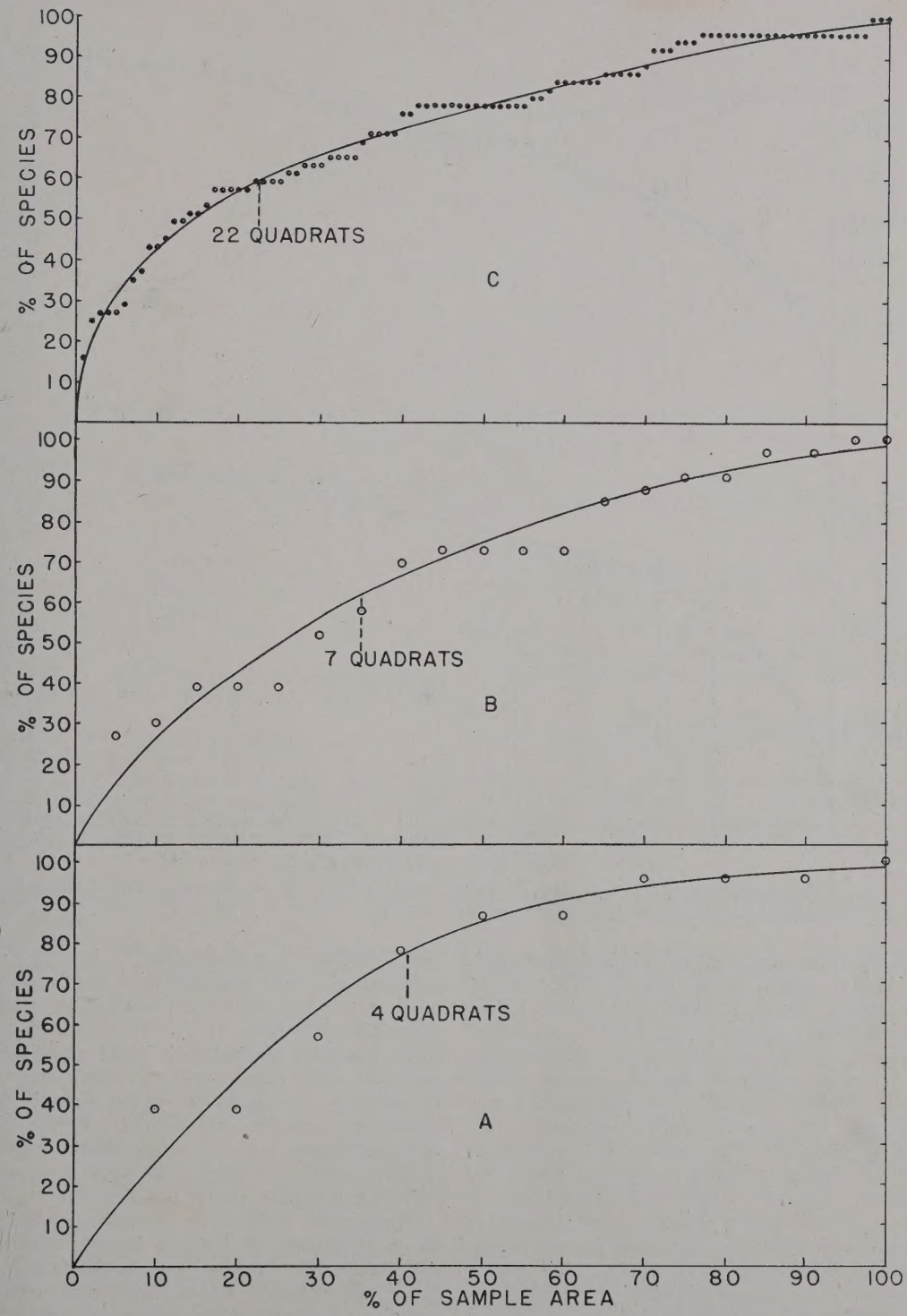

FIG. 2. Species-area curves for the McClain County prairie based on quadrats spaced evenly over the plot. The 10 per cent point moves upward with an increased number of quadrats: A, 10; B, 20; C, 100.

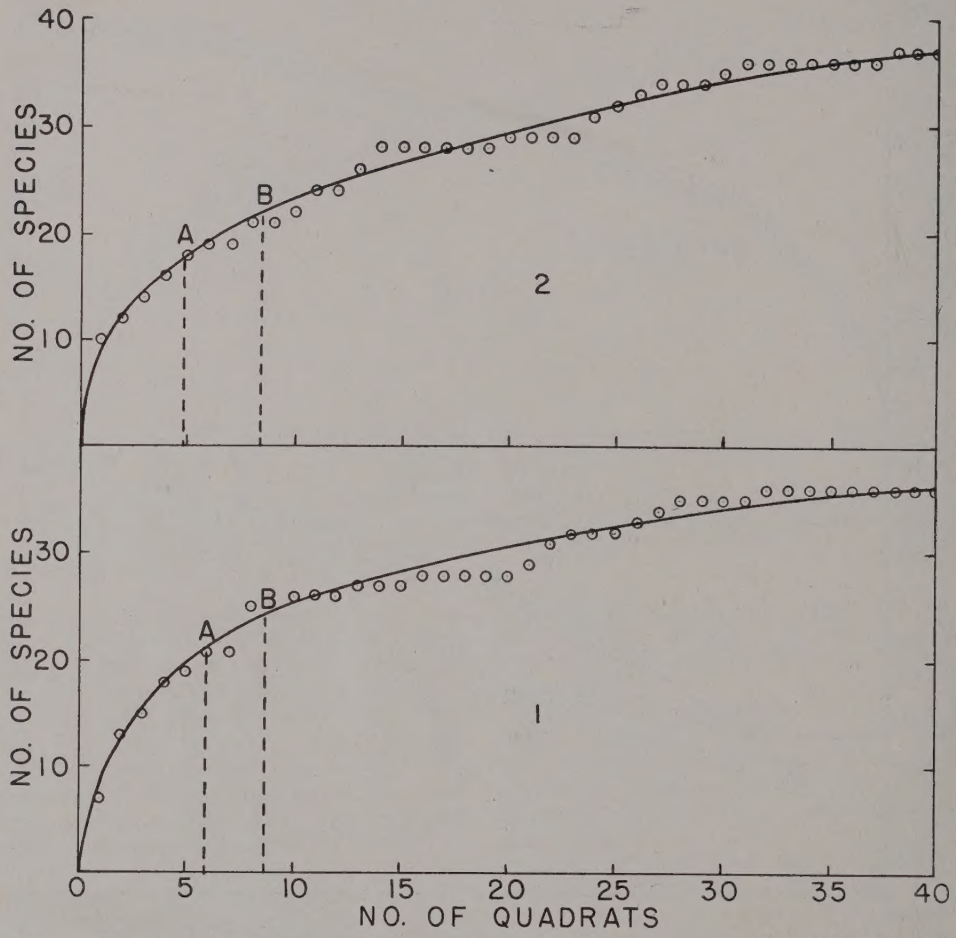

FIG. 3. Species-area curves for two different prairies in Marshall County. The 10 per cent points indicated are based on A, 20 quadrats and B, 40 quadrats.

in the past has much real value in indicating quadrat size or minimal sampling area. The work of Vestal and Heermans (1945), Penfound (1945), Vestal (1949), Cottam, *et al.* (1953), and others indicates that considerably larger samples than those usually employed are necessary for satisfactory results. Vestal (1949) suggested a new procedure for using the species-area curve to determine adequacy of sampling. The species-area curve is drawn on semi-log paper for use by his method. Then two points are located on the curve in such a way that the area represented by the second point is fifty times the area represented by the first point and the number of species represented by the second point is twice the number represented by the first point. Vestal defined the area represented by the second point as the "area definitive for composition." He felt that quantitative results obtained from two areas of the latter size in a given stand would show reasonably close agreement. If Vestal's method proves to be generally applicable, it could conceivably make the species-area curve of some real value in sampling of vegetation where reproducible quantitative results are desired. Before the above procedure can be recommended for general use, however, it needs to be tested very carefully with adequate, *unadjusted* field data.

A statistical method for determining quadrat size and adequacy of sampling is now being devised and checked by the senior author and it is hoped that sufficient substantiating data will be available soon to make the publishing of the procedure feasible.

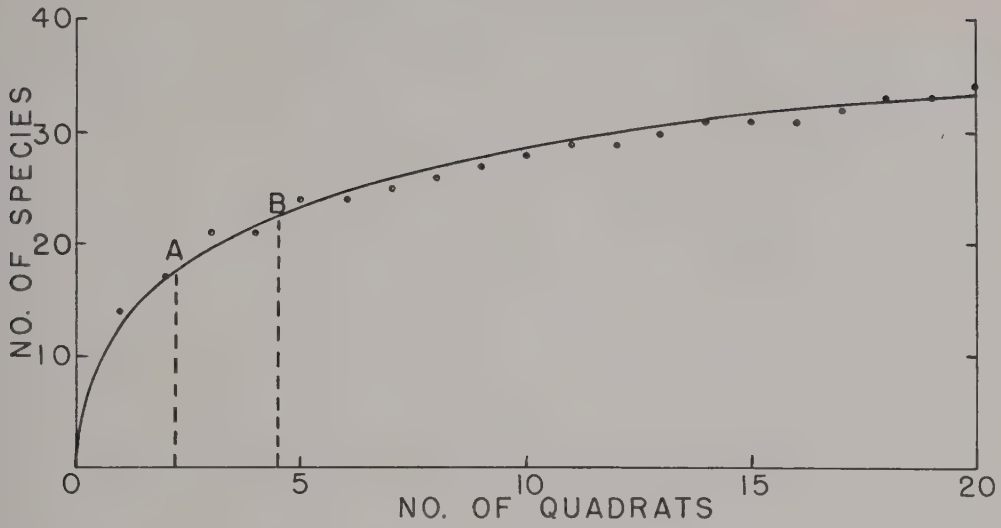

FIG. 4. Species-area curve for herbaceous species in an evergreen oak forest. (Data from Penfound and Howard 1940.) The 10 per cent point moves to the right again with an increased number of quadrats: A, 10; B, 20.

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A SURVEY OF THE ECTOPARASITES OF CERTAIN MAMMALS IN OKLAHOMA

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Introduction

Previous studies on ectoparasites have resulted in several systems of ectoparasite classification. Such classifications most frequently have been based on the phylogenetic relationships of the host animals involved and occasionally on such things as vegetational and geographical relationships. In 1950 another system was advocated by Rosicky, a Czech, who followed the ideas of the Russian authors Ioff and Tiflov (1930) by dividing the flea population of central Europe into thirteen vertical zones each of which had as its basis the vertical distribution of the habitats of the host mammals and birds.

Further, this author indicates that an association of fleas, called an aphanipterium, is an integral part of the biocenosis of the micro-habitat of the nest and represents an ecological unit. The whole of all aphanipteria in related and neighbouring zones within certain given, vertical limits is designated as a zone of aphanipteria. The primary factor in determining the vertical limits of the zone in question is the way of life of the species which form the zone and is identified according to the animal or group of animals which predominate. From these premises it may readily be observed that such zones are not static entities but on the contrary, dynamic and changing under natural conditions. These zonal divisions are subjected to many shiftings and changes which can be said to be brought about by three primary factors: 1. influences of the outer environment, 2. influences having their origin in the biology and ecology of the mammals, and 3. influences originating with the ecology and biology of the fleas.

It is hoped that this paper may, in some small way, aid in the determination of which the above mentioned methods of classification more closely represents the true conditions as they exist in the field.

This paper is taken from a portion of a thesis submitted to the Graduate Faculty of the University of Oklahoma in partial fulfillment of the requirements for the degree of Doctor of Philosophy. I wish to express my appreciation to Dr. Melvin E. Griffith under whose guidance this work was initiated and to Dr. Cluff E. Hopla under whom it was completed for their valuable suggestions and criticisms.

I would like to thank Dr. R. W. Strandtmann of Texas Technological College, Lubbock, Texas, for identification of certain genera of mites as well as confirmation of others; Dr. George P. Holland of the Department of Agriculture, Dominion of Canada, for identification of *Malaraeus* and confirmation of identification of several other species of fleas and for valuable suggestions.

Lastly, thanks are due to Mr. E. J. Greenwalt and his staff of the Wichita Mountains Wildlife Refuge who made this work possible by their cooperation and good will; to the Oklahoma Biological Survey, for making available financial aid to the author while doing field work for this study; and to Mr. Maxwell J. Wilcomb of the Communicable Disease Center of the United States Public Health Service for furnishing the transportation and trapping equipment necessary to fulfill the objectives of this project.

Description of Area

The Wichita Mountains Wildlife Refuge, where the majority of this work was done, consists of 61,480 acres of land located entirely in Comanche County, in southwest Oklahoma. This area has previously been described by Blair and Hubbell (1938), from which this description is largely taken.

The mountain range itself consists of low ridges and groups of hills extending from Fort Sill in Comanche County northwest to just beyond Granite in Greer County, a distance of 65 miles. The northern and southern limits diverge until the outlying low mountains are 30 miles apart near the center. This group of mountains is entirely surrounded by the Mixed-grass Plains district.

The mountains are made up mostly of granite and gabbro with a range of limestone hills lying along the northeast side. Many of the outliers are isolated in the plain, reaching heights of as much as 400 or 600 feet above the surrounding terrain, but the main group of mountains occupies an area in excess of 200 square miles. Many of the higher peaks of this main group exceed an elevation of 2,400 feet above sea level and rise

about 1000 feet above the plains. The lower hills are covered with a thin layer of soil but the higher peaks are bare and strewn with large boulders. There are a few caves.

The region is drained by many small streams, which flow southward into the Red River and are frequently dry except after rains. Some streams have succeeded in cutting gorges as much as 200 feet in depth. Several of these have been dammed, forming artificial lakes.

The Wichita Mountains are inclosed and penetrated by the mixed-grass plains biota which are more or less restricted to the level valley floors and flat summits in the main mountain group. The edaphic factors show a marked effect on the grassland; for example, where protected from over-grazing and not forested there is a dense growth of tall grasses and associated herbs not found elsewhere. The over-grazed lowlands consist of low, sparse, tufted grasses interspersed with *Opuntia*. The streams are bordered with a mesophytic forest composed principally of spotted oak (*Quercus shumardii*), hackberry (*Celtis laevigata* var. *texana*), black walnut (*Juglans nigra*), and American elm (*Ulmus americana*). The wooded mountain slopes are covered with a xeric forest of a scrubby nature consisting mostly of blackjack oak (*Quercus marilandica*) and post oak (*Quercus stellata*). The forest is open and interspersed with numerous glades and tufted grasses where soil permits. The north and south slopes are similar, the north being somewhat less xeric and supporting a denser growth. The higher peaks are treeless at their summits.

The climate shows an average yearly temperature of 62.0° F., and average annual rainfall of 31.53 inches, and a growing season of approximately 219 days.

Methods

The field work officially got under way on April 11, 1950 and was terminated on October 7, 1950. During this period 646 mammals were examined for ectoparasites with the following results: 304 mammals had 1638 ectoparasites representing 21 host and 23 ectoparasite species. Supplementary taxonomic work was made possible by ectoparasite collections already present in the University of Oklahoma Museum of Zoology, which increased the total number of mammals examined to 708 representing 29 species; of these, 327 were parasitized by 2317 ectoparasites representing 31 ectoparasite species and 21 host species. Trapping procedure was standardized as far as was possible in order to get comparable data from week to week and month to month. Every setting was made in the late afternoon and run early each morning before the day became warm. In this way there was little decomposition of the mammal if killed and the parasites seemed to remain on the host longer. Each trap setting consisted of from 200 to 250 traps per night or from 1000 to 1200 per week.

Mice were trapped with the standard museum special trap or the small board guillotine type mouse trap easily purchasable at any drug or grocery store. On the whole the latter type was much more successful, being a more sturdy trap and yielding a higher percentage of catches per sprung trap. The larger rodents were taken almost exclusively with the large Victor board guillotine traps. Victor steel traps from number 0 to number 2 size were used in runways and places where baited traps were unsuccessful. Box type live traps were used occasionally for nearly all types of mammals from mice to raccoons. It was found that no matter how soon certain mammals were examined for ectoparasites, none could be recovered. For example, prairie dogs, shot and examined immediately, would rarely produce ectoparasites. In these cases it became necessary to swab the nest or burrow with cotton flannel. The flannel was tied to the end of a long (four feet) flexible coil spring in such a manner that it could be inserted into the burrow, given several twists, and then pulled out. The flannel was closely inspected and the fleas, etc., removed with forceps and placed immediately in 80% alcohol or 2% saline.

Every morning when the traps were run the mammals taken were placed in closely woven sacks (one mammal per sack) and securely tied. This served the two-fold purpose of preventing the ectoparasites from escaping and allowed the trapper to carry easily a large number of mammals without hindering his efficiency. Upon returning to the laboratory these sacks were placed in tightly closed one gallon tin cans containing calcium cyanide for 15 minutes. Care was exercised not to place too many sacks in any one can in order to insure a 100% kill of ectoparasites. In the case of larger mammals such as raccoons and badgers, chloroform was used in a larger can or box.

When the fifteen minutes had elapsed the sacks were taken from the can and the mammals removed in order that data on weight, length, etc., might be recorded. The sack itself was closely examined, particular attention being given to the seams for ectoparasites which may have clung there. The mammal was then vigorously combed with a triangular file over an aluminum pan so

as to remove any remaining ectoparasites. All mites were immediately stored in vials of 80% alcohol and properly labelled. If more than five specimens of the same species of flea, louse, or tick were taken, a male or a male and a female were saved in 80% alcohol and the remainder were placed in 2% saline to be sent to the C.D.C. laboratories in San Francisco for plague examination. If less than five specimens of the same species were taken all were stored in 2% saline under refrigeration until enough specimens of the same species were taken to insure that a minimum of five specimens could be sent to the C.D.C. and one retained in alcohol for a museum specimen. Specimens could be maintained under refrigeration for a maximum of ten days before being sent to the C.D.C. or being preserved.

Several problems arose in connection with trapping and obtaining hosts by shooting. In trapping, care had to be exercised in placing the traps because of the buffalo herds which would sometimes suddenly appear and trample the traps. When setting traps in rocky areas and crevices careful attention was given to the position of overhanging rocks and ledges which could interfere with the springing of the traps. Whenever a sprung trap was found empty, the surrounding area was always searched for small mammals which might have been hit in the head by the spring mechanism. Frequently catches were taken several feet away from the traps, dead or in a state of semi-consciousness. These were most often rabbits and squirrels.

Prairie dogs presented an almost unique problem. Occupied burrows could be identified easily by watching to see which ones they entered. Unbaited and/or baited traps would then be placed around the burrow opening and left for several hours. However, it was found that as long as these traps were allowed to remain in the vicinity of the burrow the prairie dogs would not come out. Shooting was then tried by standing in the back of an open pick-up truck while the driver attempted a rapid approach. This proved relatively unsuccessful unless the prairie dog could be caught away from the burrow entrance. If shot when it was standing at the entrance or in the entrance, the animal would invariably fall dead or wounded into the hole. This then necessitated excavating the burrow by hand, a time-consuming and singularly unsuccessful procedure.

Host-Parasite Relationships

Lice have a development which during their immature stages necessitates restriction to a single species. During the developmental period of these forms on wild rodents the eggs are attached to the hairs and cannot drop off, while the immature forms hatching from the eggs remain attached and continue to feed. The adults tend to remain on one host for a number of reasons. Lice are not long-lived off the host and die almost immediately upon exposure to temperature below that to which they are accustomed. This would also partially account for the failure of a single louse species to be found on more than one species of host since predators or transients entering into abandoned nests or burrows would not be attacked by lice remaining in the nests. Another consideration not to be overlooked is the usually fatal result observed when lice are experimentally transferred from one host species to another. Death then results from poisoning, usually immediately after the first meal (Hopkins 1950). For these reasons one would expect to find a given species of louse only on a given species of mammal or on closely related species. This is precisely what was found in the Wichitas with, for example, *Hoplopleura hirsuta* being exclusively on cotton rats and *Fahrenholzia tribulosa* on pocket mice.

Fleas during their developmental period are not as intimately associated with the host animals as are lice, but when adult they are just as definitely dependent upon the host. The flea egg when laid usually rolls off the host and falls to the floor of the burrow or nest, hatches, and the larva grows and matures while feeding on the animal debris in the nest. The imago then attaches to the host for various lengths of time depending upon the species of flea, the host, and the time of the year. On the prairie dog very few fleas are ever found but swabbing of the burrow usually produces enormous numbers of fleas. Adult fleas, due to their ability to remain free from any host for long periods (25-125 days) and the acceptance, by some, of phylogenetically distant hosts frequently results in the occurrence of one species of flea on more than one species of host. This existance on several hosts may be brought about through the action of predators, the abandonment of dead hosts, the movement of the active host as well as the jumping ability of the flea.

Ticks present still another type of host-parasite relationship, in which the immature forms are often found on a host other than that of the adult form. Therefore it might be expected that different developmental stages of some species would be found on different host species. Consider the situation, for example, in the Wichitas, where the immature stages of *Amblyomma maculatum* were collected from rodents while the adult forms were

restricted to cattle and large carnivores. Also not to be overlooked is the excellent opportunity afforded by the peculiarities of the life cycle to change hosts during larval and nymphal moltings. Many immature ticks, upon completion of feeding, drop from the host, molt on the ground or vegetation, and then reattach to another host which may be in the vicinity.

The Mammalian Population and Its Ectoparasites

The mammalian population in general showed a rather low ectoparasite infestation per trapped animal. A few showed a rather high ectoparasite index but these were the exceptions rather than the rule. In almost every case some mammals were taken which were free of ectoparasites and therefore served to lower the index of infestation. In the case of *Cynomys* each burrow swabbing was considered equivalent to one animal. In table one then, the number of hosts examined would be in reality, the number of burrows swabbed.

Table I lists the total mammalian host population examined with its complete ectoparasite complement broken down into flea, louse, mite, and tick categories. Examination of this table brings out certain interesting correlations, especially in relation to the total number of ectoparasites on the host. The rather large number of ectoparasites listed for *Sigmodon* is largely an expression of mite infestation, which, if removed, would leave the cotton rats with a moderately low ectoparasite index. The raw figure of 981 ectoparasites seems to be primarily an indication of the number of hosts trapped; the ectoparasite index of 2.6 per trapped animal is rather low. The other most noticeable figure in the same column is the 728 ectoparasites on 18 coyotes resulting in an ectoparasite index of 40.4 per animal. This index is due mostly to the fleas which compose 725 of the over-all number and 40.3 of the over-all index. The condition in relation to deer and buffalo is somewhat similar with an index of 36.5 and 75.0 per host respectively and being due entirely, this time, to the tick population.

In attributing causal factors to these apparent anomalies certain conditions of data collecting should be made clear. The host specimens in the table beginning with *Canis latrans latrans* and ending with *Cervus canadensis nelsoni* were collected by biologists stationed on the refuge before

Table I. *Mammalian and Ectoparasite Indices of the Wichita Mountains area*

Hosts	No. of Hosts Examined	No. of Ecto. on Host	No. of Ecto. per Host	No. of Fleas on Host	No. of Fleas per Host	No. of Lice on Host	No. of Lice per Host	No. of Ticks on Host	No. of Ticks per Host	No. of Mites on Host	No. of Mites per Host
Cynomys l. ludovicianus	22	78	3.5	78	3.5	0	...	0	...	0	...
Citellus tridecemlineatus	10	8	0.8	8	0.8	0	...	0	...	0	...
Citellus spilosoma	1	0	...	0	...	0	...	0	...	0	...
Scalopus aquaticus	1	0	...	0	...	0	...	0	...	0	...
Dipodomys ordii richardsoni	18	4	0.2	2	0.1	0	...	0	...	2	0.1
Sylvilagus floridana alacer	2	0	...	0	...	0	...	0	...	0	...
Lepus californicus melanotus	5	16	3.2	0	...	0	...	16	3.2	0	...
Sciurus niger limitis	3	25	8.3	25	8.3	0	...	0	...	0	...
Peromyscus spp	132	50	0.4	43	0.3	0	...	3	0.02	4	0.03
Mus musculus	50	0	...	0	...	0	...	0	...	0	...
Sigmodon hispidus texianus	379	981	2.6	77	0.2	93	0.2	61	0.2	750	1.9
Pitymys nemoralis	6	17	2.8	11	1.8	0	...	0	...	6	1.0
Neotoma micropus	9	41	4.5	41	4.5	0	...	0	...	0	...
Perognathus h. hispidus	6	8	1.3	0	...	4	0.6	3	0.5	1	0.2
Perognathus flavus	2	0	...	0	...	0	...	0	...	0	...
Onychomys leucogaster	1	0	...	0	...	0	...	0	...	0	...
Reithrodontomys f. intermedius	1	1	1.0	1	1.0	0	...	0	...	0	...
Procyon lotor	1	0	...	0	...	0	...	0	...	0	...
Didelphus v. virginiana	1	0	...	0	...	0	...	0	...	0	...
Taxidea taxus	1	10	10.0	7	7.0	0	...	3	3.0	0	...
Felis domesticus	2	5	2.5	5	2.5	0	...	0	...	0	...
Spilogale interrupta	1	3	3.0	0	...	0	...	3	3.0	0	...
Canis l. latrans	18	728	40.4	725	40.3	0	...	3	0.2	0	...
Canis r. rufus	2	36	18.0	36	18.0	0	...	0	...	0	...
Odocoileus virginianus texanus	4	146	36.5	0	...	0	...	146	36.5	0	...
Antilocapra a. americana	2	5	2.5	0	...	0	...	5	2.5	0	...
Bison b. bison	2	150	75.0	0	...	0	...	150	75.0	0	...
Cervus canadensis nelsoni	1	5	5.0	0	...	0	...	5	5.0	0	...
Myotis velifer	25	Sev.	x	x	x	x	x	x	x	x	x
Total	708	2317	3.2	1059	1.5	97	0.1	398	0.6	763	1.1

this study was inaugurated and therefore do not show how many specimens were examined which were free from ectoparasites. The high indices such as 40.4, 18, 36.5, 75.0 may therefore be misleading. Final evaluation had best be left until more data are collected.

If the lower portion of Table I from *Canis l. latrans* down be ignored the highest infestation rate was found in the fleas with the mites and ticks next, followed lastly by the lice. Also the fleas were distributed over a wider range of hosts followed by the mites, ticks, and lice in order of their occurrence. (See the ectoparasite index.) This may be an expression of host specificity or preference.

The degree of infestation of any given host as shown here seems also to be affected by still another factor not yet mentioned. In addition to such an influence as host specificity, the numbers of ectoparasites on any one animal are to a certain extent governed by the size of the host animal. For example, one of the coyote hosts contained 108 fleas while one of the buffalo furnished housing for 148 ticks. In the case of small mammals, such as *Peromyscus,* it is almost impossible to conceive of them harboring as many as 148 ticks or 108 fleas and maintain a semblance of normal metabolism. From this it is apparent that the upper limits of ectoparasitic infestation may be controlled by the size of the hosts whereas the lower limits are apparently under the influence of other factors.

Ectoparasite List

This list is alphabetically arranged according to the ectoparasite and shows only the ectoparasite and hosts on which it occurred during this study.

FLEAS

Cediopsylla simplex	
Canis l. latrans	coyote
Ctenocephalides felis	
Felis domesticus	domestic cat
Ctenophthalmus pseudagyrtes	
Sigmodon hispidus texianus	Texas cotton rat
Pitymys nemoralis	woodland pine mouse
Echidnophaga gallinacea	
Sciurus niger limitis	Texas fox squirrel
Hoplopsyllus affinis	
Felis domesticus	domestic cat
Malaraeus sinomus	
Peromyscus spp.	deer mice
Reithrodontomys f. intermedius	golden harvest mouse
Myodopsylla collinsi	
Myotis velifer	cave bat
Opisocrostis hirsutus	
Cynomys l. ludovicianus	black-tailed prairie dog
Orchopeas cadens	
Sigmodon hispidus texianus	Texas cotton rat
Orchopeas leucopis	
Peromyscus spp.	deer mouse
Pitymys nemoralis	woodland pine mouse
Sigmodon hispidus texianus	Texas cotton rat
Orchopeas sexdentatus	
Neotoma micropus	wood rat
Pulex irritans	
Taxidea taxis	badger
Canis l. latrans	coyote
Canis r. rufus	red wolf
Thrassoides spp.	
Dipodomys ordii richardsoni	five-toed kangaroo rat
Thrassis fotus	
Citellus tridecemlineatus	thirteen-lined ground squirrel

LICE

Fahrenholzia tribulosa	
Perognathus h. hispidus	pocket mouse
Hoplopleura hirsuta	
Sigmodon hispidus texianus	Texas cotton rat
Hoplopleura oenomydis	
Sigmodon hispidus texianus	Texas cotton rat

MITES

Bdellonyssus bacoti	
Peromyscus spp.	deer mice
Cosmolaelaps gurabensis	
Sigmodon hispidus texianus	Texas cotton rat
Gymnolaelaps missouriensis	
Sigmodon hispidus texianus	Texas cotton rat
Haemolaelaps glasgowi	
Perognathus h. hispidus	pocket mouse
Pitymys nemoralis	woodland pine mouse
Sigmodon hispidus texianus	Texas cotton rat
Ischyropoda armatus	
Dipodomys ordii richardsoni	five-toed kangaroo rat
Macrocheles spp.	
Sigmodon hispidus texianus	Texas cotton rat
Oribatella spp.	
Sigmodon hispidus texianus	Texas cotton rat
Spinturnix spp.	
Myotis velifer	cave bat

TICKS

Amblyomma maculatum	
Peromyscus spp.	deer mice
Sigmodon hispidus texianus	Texas cotton rat
Dermacentor albipictus	
Odocoileus virginianus texanus	Texas white-tailed deer
Bison b. bison	Plains bison
Cervus canadensis nelsoni	Rocky Mountain wapiti
Dermacentor variabilis	
Taxidea taxis	badger
Canis l. latrans	coyote
Haemophysalis leporis-palustris	
Lepus californicus melanotus	black-tailed jack rabbit
Ixodes scapularis	
Spilogale interrupta	prairie spotted skunk
Bison b. bison	prairie bison
Otobius megnini	
Antilocapra a. americana	pronghorn

SEASONAL VARIATIONS

The monthly distribution of mammals trapped is illustrated in Figure 1. The months of April,

May, and August show high trapping results which may be attributed primarily to the excellent climatic conditions existing at this time during the year 1950. The low results shown in June and July were apparently due directly to the unfavorable weather conditions (1950) which prevented trap settings. The month of July had the highest precipitation on record. September and October marked the beginning of cessation of trapping for the year, hence the lower number of mammals trapped then. All other months are represented by trapping records (if any) from other investigators previously mentioned.

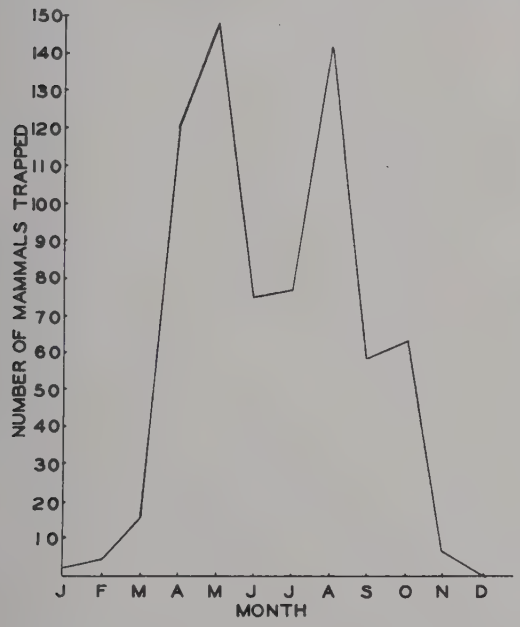

FIG. 1. Monthly distribution of mammals trapped in the Wichita Mountains.

The monthly distribution of ectoparasites is illustrated in Figure 2. It will be noted that March produced the highest number of ectoparasites and October the smallest number. A graphic comparison of the monthly over-all mammal and ectoparasite records shows a general correlation between the number of mammals trapped and the number of ectoparasites taken. Notable exceptions to this are found in the months of March, May, and November. In March it was due to the high flea index on coyotes; in May it was due to the large number of cotton rats trapped; and in November to the high tick incidence on bison and deer.

The months of June and July show a rather abrupt drop in the mammals trapped and a similar

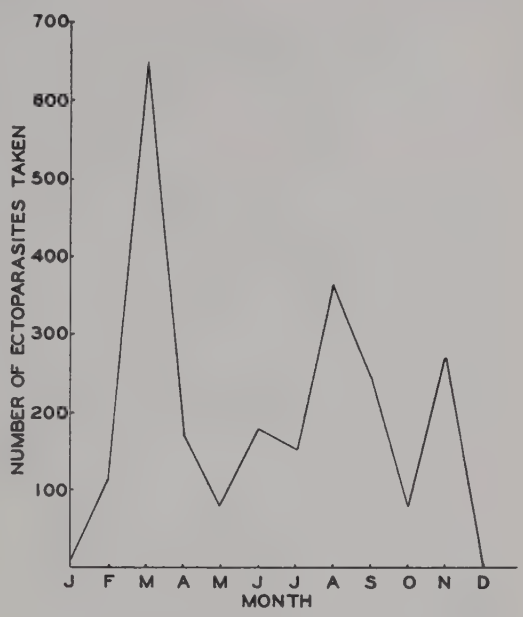

FIG. 2. Monthly distribution of ectoparasites taken in the Wichita Mountains.

drop, although not so drastic, in the ectoparasites taken. A break-down of the ectoparasite complement into fleas, lice, ticks, and mites (Fig. 3) shows that there is, in general, the same pattern in each group except the mites which show just the opposite tendency. This accounts for the moderating effect on the over-all drop in ectoparasite indices in June and July. During the actual trapping in this period the absence of other ectoparasites while mites were present was very conspicuous and raised the question as to why such a situation existed. One possible explanation is that in the colder months of the year the fleas will remain on the dead host for a considerable period of time because of the body warmth of the host but in the hot summer they tend to jump off because of the warm climate. In these warm months, excessive rain tends to cause the fleas, which have a ready means (jumping) of leaving the host not possessed by the lice, ticks, and mites, to leave the host. The ticks up to this time had not reached a high enough index to evaluate the effects of rain on their host relations but the effect, if the tick had already attached, would not be readily apparent. The mites on the other hand apparently are not as subject to the effects of external factors as are the other ectoparasites and remain on the host in spite of changes in the general environment.

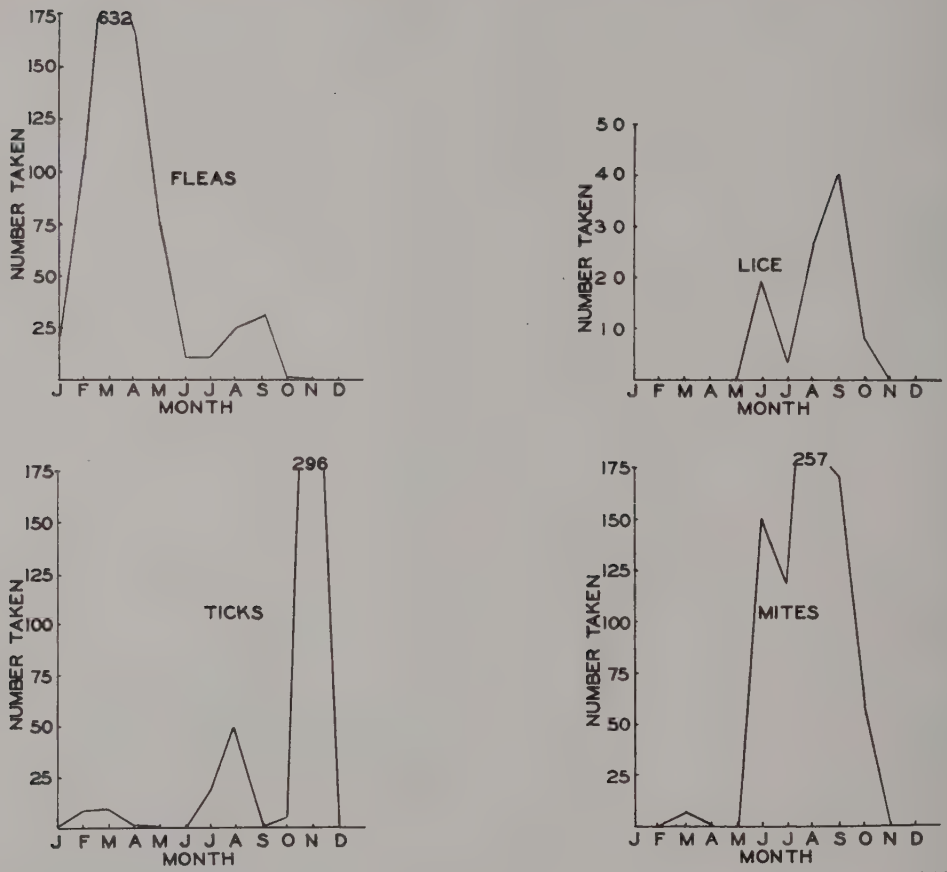

FIG. 3. Monthly distribution, by ectoparasite complement, of fleas, lice, ticks, and mites taken in Wichita Mountains.

SUMMARY

1. This study is based on collections of 2317 ectoparasites taken during the examination of 708 mammals trapped primarily in the Witchita Mountains. It includes at least 31 species of ectoparasites and 29 species of mammals.

2. Discussion covers problems in technique of mammal trapping, procurement of ectoparasites after successful trapping procedure, preservation of specimens and the ultimate disposition of the ectoparasites. A description of the Wichita Mountains area is also given.

3. A brief discussion of data is included under three main topics, (1) Host-parasite relationships, (2) the mammalian population, and (3) seasonal variations.

4. An ectoparasite list is included.

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THE RELATIONSHIP BETWEEN THE DEGREE OF SOIL PODZOLIZATION AND THE COMPOSITION OF GROUND COVER VEGETATION[1]

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This paper is one of a series of reports prepared for the purpose of promoting the use of quantitative floristic analysis in silvicultural practice. The primary aim of these reports is to reduce the subjective and frequently preconceived ocular estimates of ground cover composition. Such estimates gave raise to many unjustified generalizations and undermined the faith of foresters in floristic classifications.

Serving as an indicator of site conditions, ground cover vegetation helps the forester in the accomplishment of his daily tasks. In the survey of forest lands, the observation of ground cover plants reduces the number of auger borings and excavations necessary for the delineation of soil types. In work employing sample plots, the differences in ground cover flora often reveal concealed heterogeneity of selected study areas. Occasionally, the knowledge of floristic associations helps in the appraisal of the productive capacity of forest stands and sites, particularly those in the regions of swamp forests. The scope of these practical achievements can be considerably broadened through quantitative floristic analyses.

This study was aimed to detect correlative changes in the composition of lesser vegetation and of the soil profile. The establishment of the relationship between soils and plants was greatly facilitated by the geological uniformity of fluvial deposits in central Wisconsin. This practically level area of several thousand square miles once formed the bottom of glacial Lake Wisconsin; it consists predominantly of coarse siliceous sand only slightly modified by pedogenetic processes. The regional AC chernozem-like profile of melanized soils is typical of the prairie-forest ecotone. The differences in soil productivity brought about by succession of forest vegetation were largely erased by logging and subsequent repeated fires. At present, the significant variations in the productive capacity of soils are caused by the occurrence of sandstone substra, lenses of lacustrine clay, or ground water.

[1] Contribution from Soils Department, University of Wisconsin, in cooperation with Wisconsin Conservation Department. Publication approved by the Director of the Wisconsin Agricultural Experiment Station. The writers are indebted to Miss Martha J. Haller for assistance in the preparation of this report, and to Dr. J. T. Curtis for helpful suggestions in the course of this study.

Ground cover vegetation was studied by recording plants along a series of parallel linear transects spaced at regular intervals (Canfield 1941, Bauer 1943, Buell and Cantlon 1950). The following three aspects were considered: (1) *density* or *tally number,* given by the number of specimens of a species whose projections touch one edge of a 100 foot chain; (2) *segment frequency,* given by the percentage of 10 foot lengths in which a certain species is recorded; (3) *coverage,* expressing the percentage of consolidated cover of a certain species (Wilde 1954).

The investigated characteristics of soil included reaction, content of organic matter, exchange capacity and base saturation, bulk density, content of available nutrients, specific conductance, catalytic capacity of humus layers, degree of leaching, proximity of compacted or cemented horizons, soil air permeability, and content of soil moisture.

The study area was located near Big Flats in Adams County at the junction of the glacial outwash and a ridge of sand dunes. By virtue of an ecological accident this area includes an erratic Sphagnum peat bog whose cover of black spruce forms one of the southernmost outposts of this species in Wisconsin. The surrounding forest of 40 year old jack pine and scrub oak is supported by a complete gley podzol-melanized sand catena which is confined to the short distance of 600 or 700 feet. This compact sequence permitted a thorough analysis of both ground cover vegetation and soil.

After general examination of the area, samples of the 6 inch surface layer of soil were collected across the entire catena at 25 foot intervals, and deep trenches were excavated at strategic points for detailed study of soil profiles. On the basis of the results of analyses and examination of soil profiles, the area was divided into five genetical soil types: melanized sand, weakly podzolized sand, podzolic sand, sandy podzol, and sandy gley podzol. The profiles of these types are schematically present in Figure 1. Average results of analyses are reported in Table I.

Following investigation of soils, transects for floristic analysis were laid out parallel to soil boundaries. The width of separate soil type areas permitted the placement of at least four parallel transects at a 25 foot spacing. The average values for tally, frequency of occurrence, and coverage

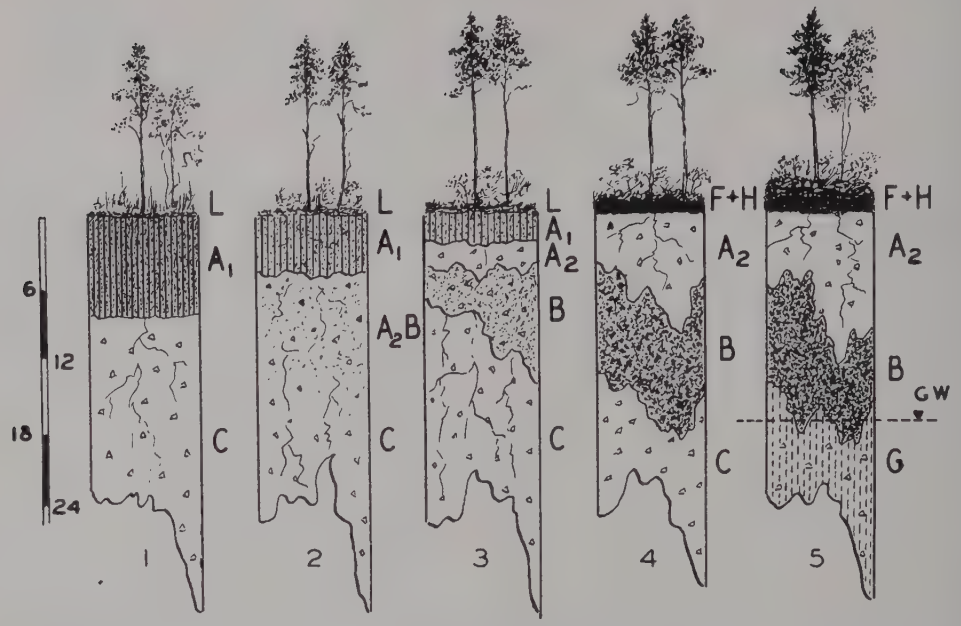

FIG. 1. Profiles of genetical soil types of a melanized sand—sandy gley podzol catena: 1. melanized sand; 2. weakly podzolized sand; 3. podzolic sand; 4. sandy podzol; 5. sandy gley podzol.

TABLE I. *Average results of physical and chemical analyses of melanized sand—sandy gley podzol catena. Results refer to the composition of the surface 6" layer unless otherwise indicated*

Soil characteristics		Melanized sand	Weakly podzolized sand	Podzolic sand	Sandy podzol	Sandy gley podzol
Reaction	pH	4.6	4.2	4.0	3.8	3.7
Exchange capacity	me/100 g	2.39	2.23	2.50	3.37	6.10
Exchangeable Ca	me/100 g	1.35	1.11	0.66	0.37	1.48
Exchangeable Mg	me/100 g	0.14	0.10	0.09	0.21	0.08
Base saturation	%	63.6	56.9	32.1	17.9	26.5
Specific conductance	mhos	4.7	6.3	4.3	7.4	17.1
Catalytic capacity	mm Hg	39	21	21	8	3
Organic matter	%	1.6	1.8	2.3	3.6	21.5
Degree of melanization	Munsell charts	7.5YR-3/0	10YR-3/1	10YR-4/1	10YR-7/1	7.5YR-8/0
Bulk density		1.01	1.00	0.98	0.83	0.75
Total N	%	0.04	0.04	0.06	0.09	0.81
Available P_2O_5	lbs/A	46	78	59	53	139
Available K_2O	lbs/A	84	72	80	96	76
Air permeability at 18" depth	mm Hg	0	0	0	12	128
Moisture content of surface layer	%	15.8	18.6	17.4	27.7	47.0
Moisture content at 24" depth	%	9.1	9.3	13.4	13.2	57.2

of different species are given in Table II. Recorded specimens of blueberries include *Vaccinium angustifolium* and *V. myrtilloides*. The separation of these two species in the field analysis was found difficult. Designation "xerophytic grasses" refers largely to *Panicum depauperatum, Koeleria cristata,* and *Danthonia spicata*. The relationship between composition of soil and the density of important members of the ground cover is presented in Table III. A similar picture of the relationship is obtained from frequency values. The latter data are omitted in this report for the sake of brevity. The analyses were performed during the summer and hence the results do not express the spring aspect of the ground cover vegetation.

Upon completion of floristic analyses, the determination of the content of soil moisture in the surface layers and lower horizons was continued at weekly intervals. The results of determinations of soil moisture at critical periods are graphically

TABLE II. *Average values for tally (T), frequency of distribution (F), and coverage of plant species on different genetical soil types of a melanized sand—sandy gley podzol catena. Figures in the "T" column marked by asterisks refer to per cent of coverage rather than tally number since the consolidated growth of these particular plants precluded recording of separate specimens. Results obtained by recording plants along twenty-one 100-foot transects laid out at 25-foot spacings*

Species	Melanized sand		Weakly podzolized sand		Podzolic sand		Sandy podzol		Sandy gley podzol	
	T no.	F %	T no.	F %	T no.	F %	T no.	F %	T no.	F %
Ceanothus ovatus	3	20	1	7						
Arctostaphylos uva-ursi	18	23	....	....	1	2				
Rosa spp.	8	50	2	13	6	44				
Fragaria virginiana	1	3	2	10	2	8				
Maianthemum canadense	1	3	2	7	18	42	....	....	5	15
Vaccinium spp.	49	90	62	100	44	84	38	97	46	90
Corylus americana	22*	70	32*	97	22*	86	9*	70	1*	18
Xerophytic grasses	33*	30	6*	30	11*	32	1*	3	3*	8
Rubus idaeus	3	7	4	13	5	12	4	17	15	40
Prunus virginiana	1	3	1	3	1	8	1	3	4	25
Pteridium latiusculum	1	3	3	23	13	38	3	17	37	80
Smilacina racemosa	2	17	2	13	3	14	1	10	4	20
Pyrola secunda	....	....	2	3						
Chimaphila umbellata	....	....	4	17	3	6				
Cornus asperifolia	....	....	1	10	3	6	2	17		
Prunus serotina	....	....	2	10	1	6	3	30		
Gaylussacia baccata	....	....	....	....	6	14	19	53	55	88
Mitchella repens	....	....	....	....	3	4				
Lupinus perennis	....	....	....	....	1	4				
Gaultheria procumbens	....	....	....	....	6	6	31	83	31	58
Trientalis americana	....	....	....	....	1	4	2	10	3	22
Rubus villosus	....	....	....	....	1	4	2	13	19	57
Aster macrophyllum	....	....	....	....	....	....	2	10		
Lonicera canadensis	....	....	....	....	....	....	4	30	3	18
Streptopus roseus	..	..	....	....	....	....	1	7	3	12
Cornus canadensis	....	....	....	....	....	....	....	....	21	48
Betula glandulosa	....	....	....	....	....	....	....	....	1	2
Smilax hispida	....	....	....	....	....	....	....	....	1	10
Sphagnum spp.	....	....	....	....	....	....	....	..	4*	12

TABLE III. *Relationship between soils and the tally number (density) of important members of the ground cover on a melanized sand—sandy gley podzol catena (Record of individual transects)*

Soil types	Transect No.	*Ceanothus ovatus*	*Arctostaphylos uva-ursi*	*Maianthemum canadense*	*Gaylussacia baccata*	*Gaultheria procumbens*	*Rubus villosus*	*Cornus canadensis*
		Tally, number of plants per 100 ft. chain						
Melanized sand	1	7	24					
	2	..	14					
	3	2	16	1				
	4	2	17					
Weakly podzolized sand	5	1	..	1				
	6	1	..	3				
	7	..	..	1				
	8	..	..	2				
Podzolized sand	9	..	1	46				
	10	..	..	16	9			
	11	..	..	16	..	13		
	12	..	..	6	15	16	3	
	13	..	..	4	7			
Sandy podzol	14	..	..	..	17	43		
	15	..	..	..	38	25	1	
	16	..	..	..	12	24	4	
	17	..	..	..	9	32	3	
Sandy gley podzol	18	..	..	2	32	69	29	22
	19	..	..	..	140	48	21	11
	20	..	..	5	32	2	17	27
	21	..	..	14	17	5	..	25

presented in Figure 2. Because the parent material of soils consists of pure quartz sand with only minute amounts of clay particles, no attempt was made to determine moisture constants. Neither was it intended to attribute to these cursory analyses a direct ecological importance. Nevertheless, obtained results show two significant details. One, the drying effect of grass on cutover areas; the sod cover even shortly after rain brought the soil moisture content below 10 per cent, thereby exhausting at least 60 per cent of water retained by forested soils. Second, the reflected influence of ground water table on the content of soil moisture following the rainfall. The writers believe that on this study area, the growth of trees and, to some extent, the distribution of ground cover plants are influenced by the depth and fluctuations of the ground water table to a much greater degree than by the content of available water retained in the upper portion of the soil profile.

The study in its entirety suggests several conclusions. The differences in soil morphology are strikingly paralleled by variations in soil reaction, exchange capacity, content of soil organic matter and total nitrogen, bulk density, catalytic effect of humus layers, and content of soil moisture. The erratic values for available nutrients, replaceable bases, and specific conductance are undoubtedly caused by the two diametrically opposed tendencies of the podzolization process—intensive leaching and the accumulation of raw organic matter, the storehouse of nutrients. The composition of soil profiles is closely correlated with both qualitative and quantitative aspects of ground cover vegetation. The distribution of several species of ground cover, particularly *Ceanothus ovatus, Arctostaphylos uva-ursi, Gaylussacia baccata, Gaultheria procumbens,* and *Cornus canadensis,* is rigorously confined to one or more adjacent members of the soil catena. Moreover, plants possessing indicator value have pronounced tendency to attain maximum density and frequency of distribution on certain genetical types of soil.

Thus, the investigation suggests that on areas with sharply differentiated soil conditions there

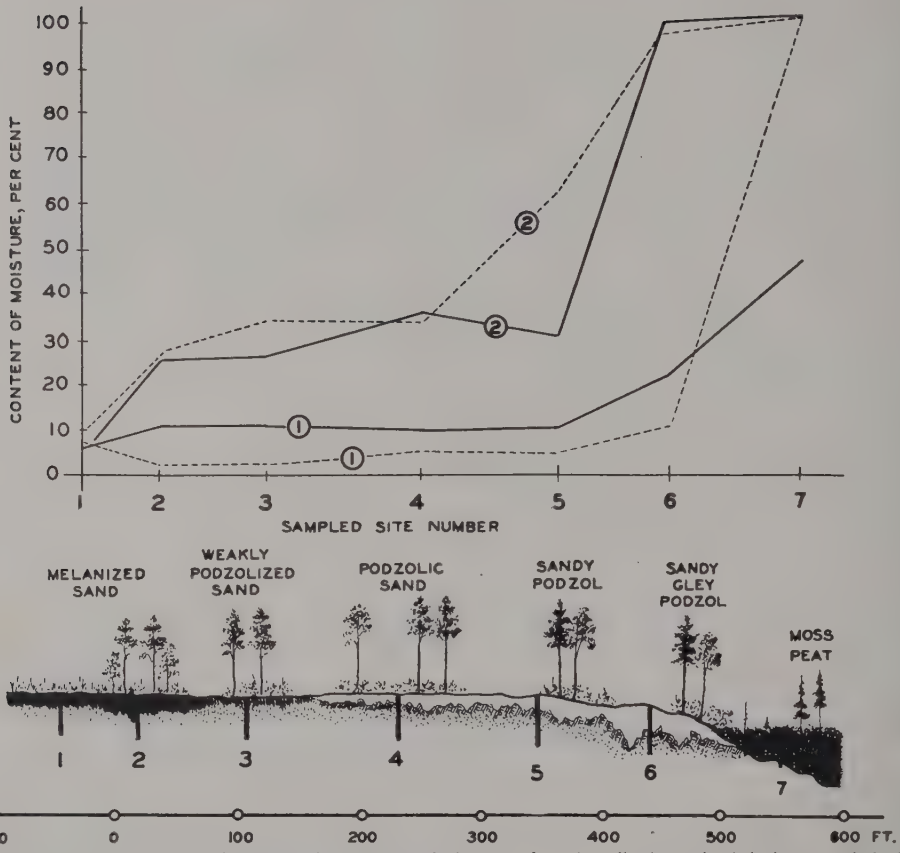

FIG. 2. Content of soil moisture in different genetical types of sandy soils determined during a period of drought (1) and following a period of rain (2). The content of moisture in the 6 inch surface layer is indicated by a solid line and that at the depth of 24 inches by a broken line. Results are expressed in per cent by volume.

is only restricted overlapping of edaphic and floristic boundaries. This picture of pronounced sectionalism in the distribution of ground cover plants owes its origin to the proverty of substratum in colloids and nutrient-bearing minerals. Under such conditions the pattern of ground cover vegetation presents a contrast to the melee of species common to fine-textured soils which are in approximately the same stage of pedogenetic development and which carry abundant supply of nutrients (Curtis and McIntosh 1951).

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LATE-PLEISTOCENE ISOLATION IN SALT-MARSH SPARROWS

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This paper[1] attempts to show the probable isolating effect of two late-Pleistocene forces on species formation in North American salt marsh sparrows of the genus *Ammospiza*. The forces considered are upwarping of the continent with reduction in weight as the ice sheet melted, and drowning of Atlantic and Gulf roast river valleys by return of glacial meltwater to the sea.

That the seaside sparrow (*Ammospiza maritima*) and sharp-tailed sparrow (*Ammospiza caudacuta*) are very closely related species needs no documentation, but it has been suggested previously by Trotter (1891), Tomkins (1941) and Montagna (1942). That they are salt-marsh derivatives of the widespread, generally freshwater, savanna sparrow seems equally evident, and current assignment of the latter to the genus *Passerculus* simply reflects that the buntings (Emberizinae) are in serious need of revision. The plumage pattern of all three is remarkably close, and there is the added similarity of song pattern, feeding habits (unusual amounts of insect or animal food for finches) and marsh habitat. The acuminate tail feathers of the sharp-tailed and seaside sparrows suggest a supporting function missing in the skulking savanna sparrow. Since seaside sparrows are intermediate in this respect, they support my view, based on general relationships, that they probably arose from savanna sparrow stock and in turn evolved sharptails.

We cannot know, of course, what the initial site of isolation of seaside from savanna sparrows was. The Mississippi Delta or embayment area must have presented a large zone of contiguous fresh and salt marsh throughout the Pleistocene, and the savanna sparrow must have ranged farther south during glacial ages. It could have withdrawn northward with the glacial recession after evolving the less cold-adapted, coastal seaside sparrow. Regarding the derivation of sharp-tailed sparrows from the latter, there is a firmer basis, for the ranges overlap today in the continuous, linear habitat of the Atlantic coast salt marsh. The fact that savanna sparrow races of the Pacific coast did not evolve the attenuate tails and slender, insectivorous bills of eastern salt marsh derivatives may be correlated with relatively small extent and recent origin of western salt marshes.

No attempt will be made to review the literature. It is best dealt with in Dwight (1898), Chapman (1899), and the later papers of Tomkins (1941), Montagna (1942) and Howell (1932). Griscom (1944) is followed for races of the seaside sparrow. These works seem to establish (Fig. 1) the following races of seaside and sharp-tailed sparrows in the continuous salt marsh habitat of Gulf and Altantic coasts:

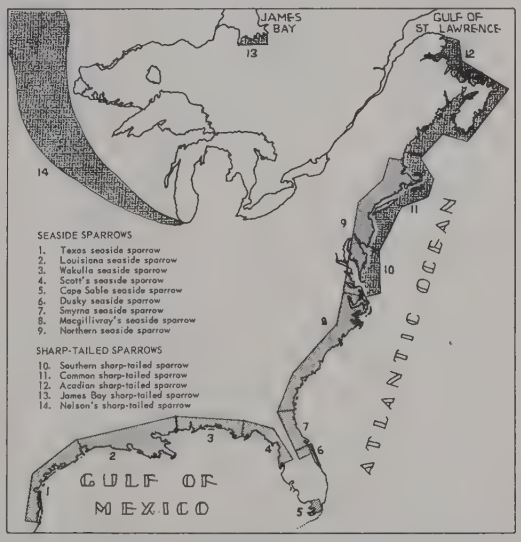

FIG. 1. Races of the seaside sparrow (*Ammospiza maritima*) and sharp-tailed sparrow (*Ammospiza caudacuta*).

SEASIDE SPARROWS

1. Texas seaside sparrow (*Ammospiza maritima sennetti*), Galveston to Corpus Christi.
2. Louisiana seaside sparrow (*Ammospiza maritima fisheri*), Southeast Texas to Pensacola, Florida.
3. Wakulla seaside sparrow (*Ammospiza maritima juncicola*), Pensacola to St. Andrews Bay (west coast), Florida.
4. Scott's seaside sparrow (*Ammospiza maritima peninsulae*), Pepperfish Keys to Indian Pass, Florida.
5. Cape Sable seaside sparrow (*Ammospiza maritima mirabilis*), Cape Sable, Florida.

[1] I am indebted to Austin L. Rand and Theodor Just for reading the manuscript and offering valuable suggestions.

6. Dusky seaside sparrow (*Ammospiza maritima nigrescens*), north end of the Indian River.
7. Smyrna seaside sparrow (*Ammospiza maritima pelonota*), Nassau County to New Smyrna, northeast Florida.
8. Macgillivray's seaside sparrow (*Ammospiza maritima macgillivrayii*), North Carolina to St. Edisto River, South Carolina.
9. Northern seaside sparrow (*Ammospiza maritima maritima*), Massachusetts to Virginia.

Sharp-Tailed Sparrows

10. Southern sharp-tailed sparrow (*Ammospiza caudacuta diversa*), New Jersey to Virginia.
11. Common sharp-tailed sparrow (*Ammospiza caudacuta caudacuta*), New Hampshire to New Jersey.
12. Acadian sharp-tailed sparrow (*Ammospiza caudacuta subvirgata*), Maine to Gulf of St. Lawrence.
13. James Bay sharp-tailed sparrow (*Ammospiza caudacuta altera*), south end of James Bay.
14. Nelson's sharp-tailed sparrow (*Ammospiza caudacuta nelsoni*), Prairie Provinces of Canada to E. South Dakota and W. Minnesota, formerly Chicago.

Nesting Habits of Salt-Marsh Sparrows

To live in the salt marshes seaside and sharp-tailed sparrows have had to make some obvious adjustments, as pointed out by Tomkins (1941). He considers the loss of territoriality in these species to be due to the non-adjacency of the nesting and feeding grounds. This is a necessary result of tidal differences of considerable range. He cites a mean tidal range of one foot in Texas and of seven to ten feet in the Savannah River marshes. Much of the marsh is, thus, unsuitable for nesting. Macgillivray's seaside sparrow bred in *Baccharis halimifolia*, the least satisfactory plant but the one that grows highest above tide, and commuted for food to the more desirable (but subject to tidal flooding) areas of *Spartina alterniflolia*. Such a situation, in combination with changes in marsh area due to tide and storm, results in widespread shifting of local populations year by year. The possibility that populations may fairly often be wiped out is suggested and these unfavorable conditions might explain the apparently low breeding potential. Atlantic and Gulf hurricanes may be a factor in present disjunct distributions, even along the Atlantic and Gulf coasts where the marsh is almost continuous. The ranges of the various seaside sparrow forms place them in greater danger from this source and may be why this species appears to have two or more broods a season in the southern part of its range. This may be necessary to make up the population deficit and northward distribution may be limited by the shorter summers.

The sharp-tailed sparrow (Fig. 1) ranges well north of the seaside sparrow but appears to be less tolerant of tidal changes. This is partly a reflection of the fact that it nests closer to the water, suspending its nest in grasses a few inches above the muck, while the seaside sparrows nest atop tussocks a foot or more high, growing out of shallow water. Sharptails evidently avoid nesting in *Eleocharis* and *Salicornia europaea*, while seaside sparrows prefer the latter as substrate. Both feed largely on the same aquatic and semi-aquatic arthropods (gammarids, etc.), deposited by daily flooding of the meadows, and both may nest side by side where the ranges overlap.

In June, 1940, Montagna (1942) found a female seaside and male sharptail *in copulo* at Tuckerton, New Jersey, so the species are, perhaps, only barely distinct. Habits, song and flight song are very similar. Nevertheless, it is clear that some differences, particularly in habitat preference, have become established, and differences in tolerance are evident from the present distribution of the two species. Everything suggests geographical isolation of seaside and sharp-tailed sparrows in the recent past and we now move to a consideration of possible Pleistocene barriers to their distribution.

Late-Pleistocene Geological Barriers

In southeastern Canada and New England marine deposits overlying glacial drift are of common occurrence. The widely accepted explanation among geologists is that the tremendous mass of the ice sheet actually weighed the earth's crust down so that marine embayments carried the Atlantic ocean far inland along the ice front. Thus, Lougee (1953) has mapped the Champlain marine stage when the sea may have extended over present Lake Champlain and even to the Great Lakes; farther north, the Ottawa marine stage is mapped as one of a series of similar marine transgressions. Of course the earth's crust tended to warp upward again as quickly as melting of the ice removed the load, so these marine embayments may have been relatively short-lived. What concerns us is that at one stage in the retreat of the ice a marine corridor evidently connected (or nearly connected) the Atlantic Ocean via the St. Lawrence river with James Bay (Fig. 2). This corridor will be discussed shortly as the route over which the north-

FIG. 2. The probable role of postglacial marine embayments in the inland distribution of James Bay and Nelson's sharp-tailed sparrows. Reference numbers as in Figure 1.

ern sharp-tailed sparrows found their way inland to the Prairie Provinces of Canada. At the same time the return of the meltwater from the Wisconsin ice sheet to the sea is agreed by geologists to have raised the level of the oceans by 230-330 feet (Flint, 1947). The large bays of the Atlantic and Gulf coasts, the result of drowning by the sea of river mouths will now be discussed in relation to the isolation of sharp-tailed and seaside sparrows.

Drowned Rivers as Coastal Barriers

The drowning of the river mouths all along the Atlantic and Gulf coasts may well have brought about the isolation, perhaps in an earlier interglacial age, of the ancestral populations that became the modern *species*, seaside and sharp-tailed sparrows. In the most recent recession of the ice the *races* of the two species may have been isolated. Delaware Bay, the drowned valley of the Delaware River and Chesapeake Bay, the drowned valleys of the Susquehanna and Potomac rivers, afford the most extensive interruptions of the salt-marsh habitat and it is in this region that the ranges of seaside and sharp-tailed sparrows overlap. The effectiveness of Delaware Bay as a barrier even today may be seen in the fact that it evidently delimits the races *A. c. caudacuta* and *A. c. diversa* of the sharptail to north and south, respectively. Chesapeake Bay (Chincoteague Inlet) may, according to Montagna, be about the southern limit of *A. c. diversa* and, therefore, of the species. The same region is evidently the rather vague dividing line between the northern seaside sparrow (*A. m. maritima*) and Macgillivray's seaside sparrow (*A. m. macgillivrayii*). The Texas seaside sparrow (*A. m. sennetti*) may have been separated from the Louisiana seaside sparrow (*A. m. fisheri*) by Galveston Bay. The latter may have been separated on the east from the Wakulla seaside sparrow (*A. m. juncicola*) when the Mississippi Delta was at times unable to keep up with the rise in sea level, allowing deep embayment of the lower Mississippi Valley. Mobile Bay may have separated the Wakulla sparrow from Scott's seaside sparrow still farther east. The Cape Sable seaside sparrow (*A. m. mirabilis*) may have been isolated when the lower third of Florida was unundated by the post glacial rise in sea level. The Dusky seaside sparrow (*A. m. nigrescens*) is in a much dissected region

of the east coast of Florida that could have been affected greatly by rise in sea level. This is also true at the northeastern end of Florida where Macgillivray's sparrow seems to be separated from the Smyrna seaside sparrow (*A. m. pelonota*). There is no point in going into the precise mechanism of isolation in each case because we cannot know exactly what conditions existed before the coastal flooding. But isolation sufficient to account for the present intergrading races appears demonstrable today.

Regarding my opinion that the sharp-tailed sparrows arose from the seaside sparrows, the initial isolation probably occurred in the region of Delaware and Chesapeake Bays. I also would not attempt to derive the southernmost race of sharptail (*A. c. diversa*) from the northern seaside sparrow (*A. m. maritima*). The common *sharptail* (*A. c. caudacuta*) resembles the overlapping race of the seaside sparrow far more closely. In fact breeding males of *A. m. maritima* are very similar in plumage pattern to *A. c. caudacuta,* though larger with duller, more diffuse coloring. But the sharply defined dark brown buff-edged scapulars of the latter are at least suggested in the former. The more acutely pointed tail feathers of the former are closely comparable with those of the latter but narrower. Thus it would appear that *A. c. caudacuta* most closely represents the ancestral stock of the sharptails segregated from the seaside sparrow *A. m. maritima*. Griscom considers birds from the center of the range of *A. c. caudacuta* to represent the mean of the species.

Postglacial Crustal Upwarp as a Barrier

Montagna points out that the Acadian sharp-tailed sparrow (*A. c. subvirgata*) shows a striking difference in habitat preference, when compared with the typical race. Scarboro, Maine, seems to be the northern limit of the latter, the Acadian race taking over to northward in the smaller, often drier, marshes of the steeper, more rocky coasts. Progressing northeastward up the coast of Maine, Montagna remarks the increased tolerance of this race toward brackish or fresh waters as the only existent marshes become those at the mouths of rivers. This becomes even more evident in New Brunswick and about the mouth of the St. Lawrence River.

A gap of 500 miles exists between the range of *A. c. subvirgata* at the mouth of the St. Lawrence and that of the James Bay race, *A. c. altera.* Today the intervening expanse of Canadian Shield has a height of land of 2000 feet, yet geologists like Richards (1936) and Nichols (1936) have described elevated beaches and marine deposits overlying glacial drift in this area. Flint (1952) has also tried to show that post-Pleistocene lakes Barlow-Ojibway and Agassiz joined a marine invasion in the present region of James Bay, but see the discussion in Deevey (1949). It is true that the facts on which Lougee (1953) bases his hypothesis of a continuous marine shoreline connecting the tops of deltas can be otherwise explained. The deltas may have emptied into fresh water lakes, in which case there would be no connected shoreline, much less a tongue of the sea covering New England.

But farther north, the case for marine connections or near-connections between James Bay and the mouth of the St. Lawrence seems better. The geological picture is strengthened somewhat by botanical work. Peattie (1922), McLaughlin (1932), Potter (1932) and Marie-Victorin (1938) report marine (halophyte) plant species inland. The beggar tick, *Bidens hyperborea,* and sedges, *Juncus Gerardi, Carex maritima* and *Scirpus rufus,* formerly ranged not only to James Bay but to Lake Manitoba, presumably via marine connections. LaRoque (1949) points out that failure to find Potter's James Bay halophytes in northern Labrador or along Hudson Straits does not rule out the possibility that they migrated over this route. But it also fails to eliminate the possibility of a marine connection between the St. Lawrence and James Bay, and his studies favor a route via Lake St. John. As Potter pointed out, the connection may never have been complete. A relatively narrow height of land might have been hopped by both halophytes and sharp-tailed sparrows.

The next race of this species, the Nelson's sharp-tailed sparrow (*A. c. nelsoni*), is found 600 miles west, breeding in the Prairie Provinces of Canada south to eastern South Dakota and western Minnesota (formerly Chicago). One wonders why there are no connecting populations between *A. c. altera* and *A. c. nelsoni* in the marshes at the southern borders of Hudson Bay, but Kindle (1923) reports enormous tidal differences here, largely dependent on winds from the north. Also, this area is subject to occasional brackishness which sharptails here may no longer tolerate. The height of land between James Bay and Lake Winnipeg (where Nelson's sparrow breeds) is, again, about 2000 feet. The occurrence of plants in Lake Winnipeg and James Bay, thought to be of marine origin strongly suggests that the sharp-tailed sparrows simply followed a postglacial marine embayment inland, then became freshwater-adapted after it disappeared. Just how well adapted they

are is questionable. Nelson's sparrow is not very abundant.

A check on the correctness of the above distribution picture may be had from the fact that both Nelson's and the James Bay sharp-tailed sparrows migrate to the Atlantic coast before proceeding south—"go back the way they came." The eastern brant (*Branta bernicla hrota*)—and formerly the marbled godwit (*Limosa fedoa*)—migrate along this east-west corridor to reach the salt marshes of the Atlantic coast, perhaps for the same reason: that it has become an instinct that persists even though the terrain has changed.

A complicating factor in trying to correlate present-day races of bird species in even so distinctive an ecological association as the coastal sea marshes lies in the fact that the cycle of glacial advance and recession occurred four times in the last million years. With regard to Atlantic coast salt marsh sparrows, it is probable that each succeeding glacial age nullified any speciation occurring as a result of river drowning by the melting of its predecessor. Any existing salt marsh sparrows would have been driven southward together by the climate. So it may be that it is only the melting of the last ice sheet that is important. Still, the separation of the Gulf coast seaside sparrows from the savanna sparrows might have occurred at an earlier advance of the ice. So might that of the sharp-tailed sparrow from the seaside sparrow, for at the time of maximum glaciation as much as 400 feet of water may have been removed from the sea (Flint 1947) to be returned in the subsequent interglacial age. Since the interglacial periods were of the order of a hundred thousand years in length, species separated by even larger drowned valleys than those along the Atlantic Coast at present, could have become very distinct before a new ice advance forced them to occupy common terrain southward.

Present Barriers

However that may be, the larger bays appear to break the continuity of the salt marsh sufficiently to interrupt gene flow between the races of both seaside and sharp-tailed sparrows. Atlantic and Gulf hurricanes may help maintain the separation of populations so well known for these sparrows. At least 110 hurricanes have devastated the Atlantic and Gulf coasts in the 60 years between 1874 and 1933, judging from Figures 32 to 39 in Tannehill (1945). Counting only the 78 hurricanes occurring south of Chesapeake Bay (those north of here are generally weaker and come late in the season), 54 are found to have struck the coasts at or near the regions of present range disjunction or at points where no seaside sparrows occur. This may not be significant and the "at or near" above makes this a very subjective judgment but it is only necessary to demonstrate a mechanism for maintaining a state of discontinuity among the populuations by periodic wiping out of colonies. This need not be always at the same point and the hurricane need not strike during the breeding season. Because of the tendency for birds to return in spring to the breeding grounds where they were born, a catastrophe at any season would reduce the breeding population of the succeeding year.

Despite the excellent work of Tomkins, Griscom and Montagna on the taxonomy of the races, these birds still present many interesting problems. Griscom's suspicion that the occurrence of darker forms of seaside sparrows is correlated with the tallest and densest vegetation seems reasonable. Humidity is higher at ground level in dense stands of grass than in sparser stands (Beecher 1942), and humid areas are generally found to produce darker races. The occurrence of light-phase individuals in dark races is, of course, outside normal taxonomic experience, though Griscom correlates these with Iva bushes in what would be much less humid situations. This raises the question whether in seaside sparrows the dark or light coloration is genetically "fixed" or whether it may be under physiological control (which of course is also genetic)—adjusting to the particular environment. Beebe (1907) was able to induce darker plumage in birds by subjecting them to greater humidity. This might be checked by holding dark and light individuals of the same seaside sparrow race captive under identical conditions and observing them for possible color change through several molts. Wolfson (1952) has demonstrated a method for obtaining several molts a year by putting captive birds alternately on long and short day periods.

Similar Distributions

It would be expected that other birds of habitat requirements similar to those of the seaside and sharp-tailed sparrows might show similar distribution in North America. Apparently there are no species with attachment to salt marsh quite so close as that met in these sparrows, but Dr. A. L. Rand has pointed out to me the rather similar range of the willet (*Catoptrophorus semipalmatus*. The eastern race (*C. s. semipalmatus*) ranges along the Gulf and Atlantic coasts as far north as Nova Scotia. The western race (*C. s. inornatus*) has an inland range something like that of Nelson's sparrow but extending as far west

as northern California and Alberta, as far south as Utah. The western race is common on the Atlantic coast in fall migration, which it may reach via the Great Lakes. Incidentally, many Nelson's sparrows apparently reach the Atlantic coast by this route, judging by Peters' review of northern sharptails (1942). In fact it cannot be assumed that Nelson's sparrow is most closely related to the James Bay sparrow. It may have reached its breeding range via a route along the postglacial Champlain Sea and the Great Lakes. But occurrence of Nelson's sparrow in fall in Maine and Massachusetts suggests that some of the migrants pass through the James Bay area. A few Nelson's sparrows have found their way to California, and of course many western willets migrate that way.

Summary

The Gulf and Atlantic coast races of seaside and sharp-tailed sparrows probably owe their initial isolation to river drowning as glacial meltwater was returned to the sea in postglacial time. The large bays thus formed interrupted the continuity of the salt marsh habitat to which they are closely adapted. The northern and inland races of the sharp-tailed sparrow—the Nelson's sparrow of the Prairie Provinces and southward, and the James Bay race—evidently could have followed marine shorelines lying just south of the ice front inland from the Atlantic. These marine invasions rapidly disappeared as the weight of the glacier diminished, but the inland races, adjusted to freshwater marshes, still persist.

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VEGETATIONAL CHANGES AND MANAGEMENT IN THE CUTOVER LONGLEAF PINE-SLASH PINE AREA OF THE GULF COAST[1]

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In recent years, forest and range research technicians in the deep South have concentrated their work on the changes in vegetation and habitat which take place under specified land treatments. They have not been greatly concerned with refinements in ecological theory and terminology. Nevertheless, the concept of secondary succession is particularly useful in the South, where the response of plants to treatment may be rapid and drastic. At the very least, such knowledge will help avoid land management practices that might be uneconomic or might lead to serious disturbance of the site or degradation of the plant cover.

This paper presents selected examples of changes in plant cover and microenvironment in relation to timber cutting, burning, and grazing in the longleaf-slash pine belt of the Gulf Coastal Plain. The area contains about 27 million acres, of which some 21 million acres are forest land. The belt is 80 to 100 miles wide and stretches nearly 600 miles from Alabama and west Florida to east Texas. Precipitation is abundant, averaging from about 45 inches anually in east Texas to more than 60 inches in southern Alabama. The frost-free growing season extends from early March to late October, and winters generally are mild.

Topography varies from nearly level in the flatwoods of the lower Coastal Plain to undulating in the pinehills of the upper Coastal Plain. Soils are mostly red and yellow podzolized lateritic types that have developed under the native pine-hardwood forests; they are strongly acid and deficient in available calcium, phosphorus, potassium, and nitrogen. On the better-drained soils, leaching is rapid and oxidation prevents much accumulation of organic matter. The subsoils are mostly fine sandy clay to heavy tough clay with slow to poor internal drainage.

The forest found by white explorers appeared fairly open, but actually was made up of moderately stocked stands of mature longleaf pine (*Pinus palustris* Mill.), with loblolly pine (*P. taeda* L.) on many of the better sites. East of the Mississippi River, slash pine (*P. elliotti* Engelm.) often predominated near the lower edges of slopes and on moister sites. Lesser woody species were oaks, hickories, and dogwood (*Cornus florida* L.). Predominant grasses were several bluestems—especially *Andropogon scoparius* Michx. and *A. tener* (Nees) Kunth—in the west, and pineland threeawn (*Aristida stricta* Michx.) in the east. Various species of *Panicum, Paspalum, Sporobolus,* and *Muhlenbergia* are present in most grass stands throughout the uplands.

CUTTING THE VIRGIN STAND

Only vestiges of the virgin longleaf pine-slash pine forest remain. In general, longleaf pine has failed to reoccupy all the areas it once dominated, especially where steam-skidding took all the larger trees and knocked down the smaller ones. Where second-growth stands did develop, the pine has been repeatedly cut, so that many areas are now occupied largely by scrub oaks, chiefly blackjack oak (*Quercus marilandica* Muenchh.), post oak (*Q. stellata* Wangenh.), and turkey oak (*Q. laevis* Walt.). Some cutover areas have come back to slash pine and some to loblolly pine. Large areas now support mainly a dense stand of grass (Fig. 1). Of the 5.6 million acres of forest land in central and southwest Louisiana, for example, more than one million is classed as clear-cut and unable to restock to pine.

FIG. 1. Cutover longleaf pine land in southwest Louisiana. Pine has failed to restock the area, so the cover is predominantly bluestem grasses. (F.S. 442959.)

FARMING

Cultivation has claimed only a comparatively small proportion of the longleaf pine-slash pine

[1] Paper presented at symposium on "Application of Knowledge of Secondary Succession" of Ecological Society of America, Madison, Wis., Sept. 9, 1953.

area, usually the moister sites with fertile soils having good internal drainage. In a few local areas, cut-over land was sold for small farms, but much of this was subsequently abandoned (Gile 1940).

The present trend is to convert some cropland to pasture by seeding improved grasses and legumes and applying lime and fertilizer. Abandoned fields usually come back to yellowsedge bluestem (*Andropogon virginicus* L.), with oak and persimmon sprouts, and if seed is available, to loblolly or slash pine, or occasionally to longleaf mixed with scrub hardwoods.

Fire

Fire has always been associated with the southern piney woods. Wahlenberg (1946) reports that, "whether started by lightning, Indians, or settlers, most of the fires were of the surface variety. . . . After settlement, probably 90 per cent of the longleaf forest burned over at least once every 3 or 4 years, on the average." Many areas burned nearly every year.

The effects of frequent burning on the chemical composition of surface soils in the longleaf pine area are considered slightly beneficial. Potassium, calcium, and other minerals are returned to the soil in readily available form. Heyward and Barnette (1934) found that repeated fires resulted in small but significant increases in soil nitrogen, attributable mainly to the decay of roots from heavier stands of grasses on burned areas that would otherwise grow up to trees and brush.

The physical properties of surface soils in the longleaf area are unfavorably affected by frequent burning (Wahlenberg, Greene, and Reed 1939). On ungrazed areas at McNeill, Mississippi, daily maximum temperatures of the surface soil during spring were 5.5° F. higher on burned than on unburned plots. Penetrometer measurements showed the burned-over soil was up to 5 times as hard as the unburned soil. Protection from fire increased water absorption slightly. Heyward and Tissot (1936) found that the layer of organic debris on unburned plots in Florida contained 5 times as many microfauna as the ground cover on burned plots, and the top 2 inches of mineral soil on unburned areas contained 11 times as many as on burned areas.

Annual winter burning of uncontrolled intensity in southern Mississippi retarded the growth of longleaf pine saplings by about one-fifth in diameter and one-fourth in height during a 5-year period (Wahlenberg, Greene, and Reed 1939). Longleaf pine seedlings that started in 1924 had 43 per cent survival on unburned and ungrazed plots 10 years later, while there was less than 5 per cent survival on annually burned plots. However, scrubby oaks and hardwood shrubs, particularly gallberry (*Ilex glabra* (L.) Gray) encroached on unburned plots, while annual burning held this hardwood growth well in check. On unburned areas, the accumulated dead vegetation and pine needles had a smothering effect on herbs and grasses, so that only a scattered stand of little bluestem remained. Annual burning permitted an increase in slender bluestem and in native legumes such as species of *Lespedeza* and *Desmodium*.

A thirty-two year study in central Louisiana gave similar results (Bruce 1947). An ungrazed, annually burned area was almost pure longleaf pine, with little brush and about 1,000 pounds of grass per acre, mainly little bluestem. The unburned area, in addition to longleaf pine, had much loblolly pine and shortleaf pine (*P. echinata* Mill.) and considerable southern red oak (*Quercus falcata* Michx.), blackgum (*Nyssa sylvatica* Marsh.), sweetgum (*Liquidambar styraciflua* L.), flowering dogwood, and many species of brush. Grass averaged only about 30 pounds per acre.

Heyward (1939), who examined 51 long-unburned forests of longleaf and slash pine, found that hardwoods were numerous in practically all longleaf pine stands of pole size or larger from which fires had been excluded for more than 10 years (Fig. 2).

Wildfire, and even controlled annual burning are obviously too damaging to forests. At the same time, the trend under complete fire protection is toward a mixed pine-hardwood-brush association considered undesirable by foresters, range managers, and wildlife managers alike. Some degree of burning seems essential in the silviculture of longleaf pine (Chapman 1926, Garren 1943). Of necessity, therefore, foresters have developed the technique of prescribed burning, in which fire is used carefully to accomplish a specific purpose on a definite area.

Connaro (1942) pointed out several specific purposes for which fire can be used in longleaf pine-slash pine forests: ". . . in preparing seedbeds, for planting-site preparation, for insects and rodent control, for elimination of plant diseases and weed species, for protection from wildfire, for grazing, for naval stores operations. . . ." Bickford and Curry (1943) worked out detailed instructions involving analysis to determine the desirability of using fire, and plans for treating individual burning units.

On nearly 1,000 acres of cut-over land in central Louisiana, prescribed burning prior to seed-

FIG. 2. Pine-bluestem cover on left, after 10 annual winter burns. Pine-hardwoods on right, after 25 years of protection from fire. (F.S. 442968.)

fall was used to improve the catch and increase survival of longleaf pine seedlings (Bickford and Bruce 1948). Burning once or twice after the seedlings were a year old gave better survival than no burning or annual burning.

The effectiveness of prescribed burning for disease control was shown by another experiment in central Louisiana (Wakely and Muntz 1947). One area was burned in winter, 3 years and again 6 years after planting to longleaf pine. A comparable area was unburned. At 11-½ years after planting, tree survival was about the same on the two areas, but on the burned area 64 per cent of all living trees were above 4-½ feet in height, as against only 22 percent on the unburned area. Most of the superior height growth on the burned area seemed due to the effectiveness of the fires in controlling brown spot needle disease without seriously injuring the longleaf pine seedlings.

The relative effects of annual burning *vs.* prescribed burning on grass, forbs, and other understory vegetation are not yet clear. Halls *et al.* (1952), reporting on a 7-year study in southern Georgia, found no marked difference in the response of vegetation whether one-third, one-half, or all of a range was burned each year.

GRAZING

Livestock grazing is a major factor in secondary succession on cut-over longleaf pine and slash pine lands. Important aspects are kind of livestock, and season and intensity of grazing.

Cattle, sheep, and hogs graze almost at will in the "free range" area from Mississippi to east Texas (Alabama and Florida have passed livestock fence laws within the past three years). Hogs, in particular, prevent or retard the development of young longleaf stands, by eating the seed and rooting up seedlings. They also strip the thick bark from lateral roots and girdle young saplings. The damage occurs mainly in spring, when carbohydrate content of the bark is as high as 80 per cent (Hopkins 1948). There are numerous places in Louisiana where protection by a hog-proof fence has allowed natural or planted pines to grow into a new forest, while outside the fence the cut-over land remains predominantly open (Fig. 3). In some areas, the hungry hogs turn to slash and loblolly pine roots and lower stems when longleaf pine is not present.

Sheep may seriously retard development of young natural and planted stands of longleaf and slash pines by nipping the terminal and lateral buds of seedlings and small saplings, especially in winter and early spring when most other vegetation is dry and unpalatable (Maki and Mann 1951). The present recommendation is to exclude sheep from young natural or planted pines during winter and spring until the trees are at

FIG. 3. The fenced area at the left has an excellent stand of young longleaf pine seedlings. Outside of the fence hogs completely prevented seedlings from becoming established. (F.S. 442962.)

least 4 feet tall and past the size at which they are liable to injury.

Trees and cattle have been a natural combination in the Gulf Coastal Plain for more than 300 years. Cattle rarely damage pine seedlings unless there are too many animals or green forage is scarce—as during winter and early spring, especially on freshly burned range (Campbell and Cassady 1951). Moderate grazing in spring and summer on ridges and slopes in the pinehills allows the trees to grow with little grazing disturbance, and the grass cover to be gradually dominated by little bluestem and associated species. Even moderate grazing in winter, however, tends to open up the stands of such palatable woody shrubs as Elliott blueberry (*Vaccinium elliottii* Chapm.), shining sumac (*Rhus copallina* L.), and sweetleaf (*Symplocus tinctoria* (L.) L'Her.).

Heavy grazing, especially when combined with annual burning, is another story. Under these conditions, Wahlenberg, Greene, and Reed (1939) reported for McNeill, Mississippi, a gradual decline in little bluestem, and an increase in slender bluestem and carpetgrass. This change in cover was accompanied by considerable soil compaction and reduced water absorptive capacity.

In central Louisiana, plots that received close artificial harvesting every 2 weeks produced 41 per cent (by weight) less grass than undisturbed plots (Cassady 1953). The grass was predominantly pinehill bluestem (*A. divergens* (Hack.) Anderss.). It was concluded that the ill effects of one year of close repeated harvesting on this species may last for several seasons, even under subsequent complete protection from grazing.

Examples have been noted in Louisiana where landowners purposely grazed certain areas closely in order to encourage the spread of carpetgrass, which provides a longer season of grazing than do the bluestems alone. Such changes, brought about by drastic use, probably represent unfavorable ecological development, but it is still an open question as to whether they are undesirable economically. Williams (1952) has summarized these changes of herbaceous cover in terms of poor, fair, good, and excellent range condition.

FOREST-RANGE RELATIONSHIPS

Large areas of cut-over land in the Coastal Plain are in process of growing new pine forests, either through natural reproduction or through planting or direct seeding. The effects of the development of such tree stands on the herbaceous understory have been reported by Bond and Campbell (1951a). Average cut-over land produces

about 1,500 pounds of grass per acre (air-dry). There is only a slight reduction in grass weight under slash pine plantations for the the first 8 to 10 years. But by the 12th to 15th year, grass production is reduced to about 300 pounds per acre. After this time, if the trees are thinned at 5-year intervals and periodic prescribed burning is practiced, grass production is expected to increase gradually, reaching about 700 pounds per acre by the time the pines attain nearly full height and the stand is more open at age 60.

Relationships of grass and forb production to ecological factors have been reported for southern Alabama pine hills by Gaines *et al.* (1954). Herbage production is closely associated with weight of tree litter. Mean herbage production per acre (adjusted to average litter weight) is highest on soils with clay subsoils, and lowest on deep sands. Distribution of the tree stand is also important; a single isolated longleaf pine influences grass production only 6 to 8 feet from the trunk, while a group of trees reduces herbage production up to 30 feet away from the forest wall.

An important part of forest management in the South is the removal of undesirable hardwoods that interfere with survival and growth of young pines. On an experimental area with an average of 330 blackjack oaks per acre, pines were planted and the hardwoods were poisoned. This treatment not only allowed better survival and growth of the pines, but during the first season the grass on treated plots was conspicuously greener and remained green longer than on untreated plots (Fig. 4). By the end of the third year, grass production had more than doubled (Cassady 1952).

Fig. 4. After being released from an overtopping heavy stand of scrub oaks, both grass and planted pines grew rapidly. (Louisiana Forestry Commission.)

Problems

The foregoing examples indicate the trend of management of cut-over longleaf pine-slash pine land in the Gulf Coast area for second-growth pine and for range forage. However, as management becomes more intensive on soils with limited plant nutrients, ecological problems multiply. The virgin longleaf pine stand was a relatively stable association; the large trees lived for 150 to 300 years. Foresters now plan on rotations of 65 to 75 years for sawlogs. Some even visualize clear-cutting for pulpwood at about 30 years of age and replanting or seeding to fast-growing strains of pine. Can such intensive cropping of the soil continue without use of commercial fertilizer to make up for decreasing soil nutrients? Do hardwoods have any place in good management of this land, and if so, which species?

In time, will the physical properties of the soil be so modified by fire and close grazing as to hinder reproduction and growth of both the trees and the grass? What combination of season and intensity of cattle grazing will bring about the highest production and best variety of forage under the prevailing forest management systems? At what stage in the secondary succession does competition from scrubby hardwoods become limiting to pines and how should this problem be met? These and similar questions bid fair to keep applied ecologists in the South fully occupied. A better knowledge of secondary plant succession is basic to effective work in this field.

Summary

Secondary plant succession in the longleaf pine-slash pine belt of the Gulf Coastal Plain is influenced by timber cutting, burning, and grazing. The damaging effects of wildfire and of uncontrolled annual burning are in part alleviated by their replacement in managed stands by prescribed burning, which is useful in reproducing and growing longleaf pine and slash pine stands and in improving grazing. Hogs and sheep are serious threats to the early survival and growth of both longleaf and slash pines, but cattle usually allow the stands to develop with little disturbance.

The scrubby hardwoods and underbrush that naturally develop when only the pines are cut

or when complete fire protection is practiced constitute a problem on which more and more attention is being focused.

Increasing intensity of land management for timber growing and range grazing is aggravating conditions of soil fertility and physical condition which may soon be reflected in stand structure and growth of both trees and grass. These problems should be attacked from the ecological viewpoint.

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DIFFERENTIATION OF NUTRITIONAL PREFERENCES IN BRAZILIAN SPECIES OF DROSOPHILA[1]

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Introduction

When two or more sympatric species subsist on the same type of food, they are likely to compete with each other when the food supply becomes a limiting factor. Natural selection may then be expected to lessen the competition between species through divergence in the most preferred kind of diet. The divergence may or may not reach the point of rigid specialization (monophagy). Monophagy is advantageous if the food which each species requires is uniformly abundant, since monophagous species which have different diets do not compete for food. But when some kinds of food are from time to time in short supply, too rigid a specialization endangers the existence of species which depend on a single kind of nutrition. Natural selection may then be expected to strike a compromise. If the abundance of different foods fluctuates widely, sympatric species which subsist on these foods should choose different foods when choice is available but should

[1] Contribution No. 13 of the cooperative research project of the University of São Paulo and Columbia University on genetics and ecology of tropical Drosophila.

be able to maintain themselves also on the less preferred kinds of nutriment.

Exploratory studies on the food habits of various species of Drosophila disclose a situation which is in accord with the above theoretical deductions. Carson (1951), da Cunha, Dobzhansky, and Sokoloff (1951), Dobzhansky and Pavan (1950), Pavan (1952), Shehata and Mrak (1952), Wagner (1944, 1949), and others found that most or all species of Drosophila are able to feed on a variety of fruits and other fermenting substances, and that every species of yeast tested in this respect attracts a variety of species of Drosophila. And yet, every species of Drosophila prefers some foods to others, and every species of yeast is visited by a quantitatively different assortment of Drosophila species. All Drosophila are, then polyphagous but each has its own set of preferences.

These findings raise a series of new problems and suggest many experiments to be made. If the divergence of food preferences is brought about by the above method, then the divergence should be greater when the competing species are numerous, and less when only few sympatric species share a habitat. By and large, more sympatric species of Drosophila live together in tropical habitats than in temperate ones, and the variety of foods for Drosophila is also greater in the tropics. One can, accordingly, make a working hypothesis that the food preferences among tropical species should be more marked than among temperate ones. The same species of Drosophila may in different parts of its geographic distribution area come in contact with different competitors. From this follows another working hypothesis: some species of Drosophila may be divided into races with different food preferences.

The experiments reported in the present article were undertaken in order to test the above working hypotheses. The results obtained are, however, merely indicative and not conclusive. More work will have to be done. Perhaps the most valuable result of the work so far carried out is the development of an experimental technique that may be serviceable in the future.

The Yeasts

The yeasts used in the experiments were isolated from the crops of two very closely related species, *Drosophila willistoni* and *D. paulistorum,* collected in the Cantareira forest preserve near São Paulo city in Brazil. The flies were attracted to bait which they were unable to ingest, their crops were taken out, and the microorganisms found inside were grown on agar plates, as described by Shehata and Mrak (1951) and by da Cunha, Dobzhansky, and Sokoloff (1951). Altogether about 69 isolations of yeasts were made, 51 of them from *D. willistoni* and 18 from *D. paulistorum.* Amongst these, two yeasts (isolation Nos. 29 and 51) which seemed to occur most frequently in the crops of *D. willistoni,* and two (Nos. 54 and 82) which were frequent in the crops of *D. paulistorum* were chosen for the experiments. Unfortunately it was after the field work had been completed that we found that three out of the four yeasts chosen, Nos. 29, 51, and 54, belonged to the same species—*Candida Krusei* (Cast.) Berkhout. The fourth, No. 82, is *Kloeckera apiculata* (Reess Klöcker) Janke. We are greatly indebted to Professor H. J. Phaff for the determination of these yeasts. Although Nos. 29, 51, and 54 are not appreciably different by any of the standard tests used in yeast systematics, and must accordingly be classed in the same species and variety, it will be shown below that some species of Drosophila are able to discriminate between them.

The yeast strains are conserved on slants of Difco wort agar, kept in a refrigerator. For experimental purposes the yeasts are inoculated into flasks with 250 cc of malt-nitrogen base-dextrose medium and permitted to grow for about 24 hours at room temperatures, which in tropical Brazil are usually high enough to give a rich suspension even without aeration. The yeast suspensions are then inoculated into autoclaved banana, as explained below.

Attraction of the Flies

Da Cunha, Dobzhansky and Sokoloff (1951) exposed cups with absorbent cotton soaked in suspensions of various yeasts. When such cups were exposed in the forests of the Sierra Nevada of California, fair numbers of Drosophila flies were attracted to them. A similar technique was tried in the equatorial rainforests near Belem, but it soon became apparent that few flies are attracted, presumably because of the competition exercized by the fermenting fruits and other substances which are abundant in tropical forests. We then resorted to using banana bait fermented with the yeasts which we desired to test. Approximately 10-15 liters of mashed ripe banana were autoclaved, and upon cooling inoculated with the suspension of one or the other of the four yeasts mentioned above. In about 24 hours intense fermentation was obtained, the smell of the bait being sensibly different with different yeasts, even for human olfactory organs.

The bait was then exposed on the forest floor,

cleared of twigs and other obstacles for the subsequent collecting. Each bait consisted of roughly a pound of the fermenting mash, placed in a small pile so as to prevent it from either drying or being washed away by rain. The baits were arranged either in a line or in a circle, the distance between the neighboring baits being approximately 10 to 20 meters. The baits fermented with the different yeast were always used in the order 29-51-54-82-29-51, etc. The flies begin to be attracted to the bait almost immediately. The collecting was made on two successive days by sweeping with a collecting net over the bait and placing the flies caught in numbered vials. At the end of the second collecting the baits were destroyed by covering them with soil; the same terrain was used for experiments after an interval of no less than five days, and then the order of the baits was changed. The flies collected were taken to a laboratory and classified as to species. Some groups of sibling species cannot be distinguished easily; then only the species group was recorded (for example, the "*willistoni* group").

Autoclaved banana not fermented with yeast attracts no Drosophila for several hours and few for at least two days after being exposed as bait. This makes it probable that the yeast attracting the flies to the fermenting bait is the yeast being tried. The large numbers of flies which come to the fermenting bait are, then, attracted by the odors resulting from the fermentation, and as indicated above these odors depend upon the yeast used. The preformance of a bait depends, therefore, on the yeast as well as on the substance fermented (Dobzhansky and Pavan 1950, Pavan 1952); in our experiments the substance fermented was the same.

The Collecting Localities

Four regions of Brazil were selected in order to compare the food preferences of species of Drosophila in environments which differed in climate as well as in the composition of their native faunas of Drosophila. On June 10, 17, and 22, July 11 and 15, August 9 and 22 and September 10, 1952, bait was exposed in three localities in the vicinity of Belem, State of Pará. This is a region of equatorial rainforests (Amazonian Hylaea). On July 18 and 21 similar experiments were carried out in two localities near Fordlandia on the Tapajos River, State of Pará. This is also a rainforest of the Amazonian type, but with more pronounced wet and dry seasons than at Belem. On September 4 we worked in a forest on the Itambacuri, a tributary of the Rio Doce, State of Minas Geraes. Here a dry facies of the South Brazilian coastal rainforest is encountered, with many species of Drosophila which are common in Amazonia being rare, and *vice versa*. Finally on January 5-7 and 13-14 the collecting was made at Cantareira, near São Paulo. This region has a relatively cool climate characteristic of the landward declivity of the Serra do Mar in Southern Brazil. The yeasts used in the experiments were isolated from flies caught at Cantareira a year earlier.

Statistical Treatment of the Data

Baits placed ten or more meters apart may attract different assortments of species of Drosophila. A given fly species may be numerous on one bait and rare on the next; or else, the numbers of individuals may be similar, but a given species may represent different proportions of the total catch of Drosophila on different baits. Such differences cannot be ascribed only to the yeasts with which the bait is fermented, because differences are often observed when the bait is uniform. The local, microgeographical variations in the abundance of Drosophila arise from an uneven distribution of their natural foods, and, possibly, from other unknown factors (Dobzhansky and Pavan 1950; Pavan 1952).

We therefore chose as the unit of observation a series of four neighboring baits fermented with the four yeasts used. The number of individuals of each species of Drosophila collected on each bait is then expressed in percentages of the total number of this species found on the four baits of the series. This percentage becomes, then, a single variate. The percentages obtained for the same species in different series of baits are then averaged and the mean percentage used as a measure of the attractiveness of a given species of yeast to a certain species of Drosophila. It is evident that the quality of the data depends to a great extent on the number of series of baits studied in a given locality. An experienced collector is able to take care of 6 to 12 baits, depending on the quality of the terrain and other factors. Our working team consisted of two to four collectors, so that at most 10 to 12 series of baits could be made on one day. The data are summarized in Table I. Mean percentages and their standard errors are given for all species which were reasonably common. Apart from these, about 30 species were recorded but were too rare to yield significant data.

A difficulty arises with the moderately common species, since the number of individuals collected on the four baits of a series may be small. We have arbitrarily chosen 10 as the minimum num-

TABLE I. *Percentage frequencies of flies of a given species collected on each of the four yeasts used in the experiments*

Species	Locality	Flies Counted	Series	Yeast No. 29	51	54	82
Willistoni group	Belem	5832	31	13.5± 2.1	13.4± 2.1	12.3± 2.1	60.8± 3.1
Willistoni group	Tapajos	1983	12	23.0± 3.6	13.4± 1.2	8.5± 1.6	55.1± 3.2
Willistoni group	Rio Doce	8508	11	8.6± 2.8	11.7± 2.4	13.0± 2.6	66.7± 7.0
Willistoni group	São Paulo	1743	24	14.0± 2.5	10.7± 2.2	14.6± 2.5	60.6± 3.7
Sturtevanti	Belem	188	12	21.4± 3.5	37.8± 4.0	10.3± 2.6	31.1± 3.9
Sturtevanti	Tapajos	218	9	28.7± 4.7	39.9± 6.8	12.3± 3.2	19.1± 3.5
Sturtevanti	Rio Doce	59	4	9.0± 5.3	28.5±10.3	4.3± 2.0	58.2±14.8
Polymorpha	Belem	21	2	17.5	4.0	4.0	74.5
Polymorpha	Rio Doce	1375	8	16.2± 4.2	17.4± 4.2	16.3± 4.6	50.1± 7.6
Polymorpha	São Paulo	437	20	22.2± 2.4	26.3± 2.8	22.9± 2.5	28.5± 3.1
Nebulosa	Tapajos	162	8	43.6± 5.2	7.4± 1.6	6.4± 1.6	42.6± 4.9
Nebulosa	Rio Doce	65	5	19.6± 5.7	5.6± 2.5	13.2± 5.0	61.6± 4.0
Nebulosa	São Paulo	62	5	12.6± 4.9	13.8± 5.2	21.4± 7.1	52.2±11.2
Griseolineata	Rio Doce	146	6	16.1± 5.4	9.3± 5.1	8.3± 2.7	66.3± 9.5
Griseolineata	São Paulo	2065	23	21.8± 2.6	25.6± 2.8	24.4± 2.5	28.2± 2.8
Fumipennis	Belem	956	9	28.1± 5.4	21.4± 3.7	9.8± 3.2	40.7± 5.5
Camargoi	Belem	688	11	25.5± 4.0	16.8± 3.8	14.8± 2.0	42.6± 4.1
Neotanygastrella	Belem	215	10	8.0± 2.7	10.0± 2.8	17.6± 3.6	64.4± 5.6
Para	Belem	441	6	4.1± 1.9	3.1± 1.2	8.6± 5.0	84.3± 5.2
Mirim	Belem	92	5	31.0± 7.0	29.6± 9.8	19.4± 7.6	19.8± 9.6
Flavoreplata	Tapajos	169	6	38.5± 9.5	22.7± 8.8	15.0± 7.6	23.7± 9.0
Neocardini	Rio Doce	1258	8	15.7± 4.6	16.3± 4.7	16.9± 4.7	51.2± 7.3
Cardinoides	Rio Doce	134	6	56.7± 6.8	10.5± 2.4	13.8± 2.6	19.0± 3.2
Simulans	Rio Doce	301	8	20.3± 6.8	17.8± 4.0	8.0± 3.5	53.8± 6.5
Capricorni	São Paulo	702	23	20.2± 2.7	15.8± 2.6	15.5± 2.8	48.5± 3.6
Guaramunu	São Paulo	489	16	17.6± 3.3	23.6± 4.0	29.8± 4.9	29.0± 4.8
Calloptera	São Paulo	275	11	19.1± 4.6	19.0± 4.6	33.3± 4.9	28.6± 4.9

ber of flies of a species on four baits of a series. When the numbers fell below 10, the flies caught on two or three adjacent series of baits were combined and treated as a single series. For this reason, the numbers of series recorded in Table I are different for different species from the same collecting locality. Thus, in the vicinity of Belem, 31 series of observations were made, but only the *willistoni* group of species was sufficiently frequent to utilize every series. For other species (see Table I) some series had to be combined, thus decreasing the number of percentages which served for the calculations. It should also be realized that an individual percentage may be based on different numbers of flies—from ten to several hundred.

DROSOPHILA SPECIES WHICH PREFER THE KLOECKERA YEAST

Examination of Table I shows that baits fermented with different yeasts are not equally attractive to certain species of Drosophila. If the four yeasts were equally attractive, each bait would yield about 25 per cent of the total catch, within the limits of sampling errors. The *Kloeckera* yeast (No. 82) attracts significantly more than its share of *D. willistoni* group, *D. nebulosa* Sturtevant, *D. fumipennis* Duda, *D. camargoi* Pavan, *Neotanygastrella chymomyzoides* Duda, *D. para* Pavan & Burla, *D. neocardini* Streisinger, *D. simulans* Sturtevant, *D. capricorni* Dobzhansky and Pavan, and also of some of the rarer species which are not included in Table I because too few individuals have been collected. The preference for *Kloeckera* appears to be strongest in *D. para* since 84 ± 5% of the individuals chose this bait, and only 16% the three other ones.

DROSOPHILA SPECIES WHICH SHOW NO PREFERENCE

Several species have evinced no clear preference in choosing between the yeasts offered in our experiments. To this category belong *Drosophila mirim* Dobzhansky and Pavan, *D. guaramunu* Dobzhansky and Pavan, *D. calloptera* Schiener, and possibly *D. griseolineata* Duda. This behavior does not mean that these species have no nutritional preferences of any kind The experimental data show only that they do not discriminate between the two yeast species which happened to be used in the baits offered. They may be quite capable of differentiating between other yeasts.

RACIAL VARIATION IN FOOD PREFERENCE

Only five species were obtained in sufficient numbers from more than a single geographic region to permit comparison of the food preferences of races of the same species. Among these, four

species yielded data which suggest that the food preferences are not constant throughout the species distribution area. The Rio Doce population of *Drosophila polymorpha* Dobzhansky and Pavan clearly prefers the *Kloeckera* bait (No. 82) to that with the *Candida* yeasts. In seven out of eight series the *Kloeckera* bait attracted greater numbers of flies than any of the *Candida* baits. *D. polymorpha* is rare at Belem and in the Tapajos, but the few individuals collected there attended mostly the *Kloeckera* bait. And yet, at São Paulo *D. polymorpha* came to the four baits indiscriminately (Table I, Fig. 1).

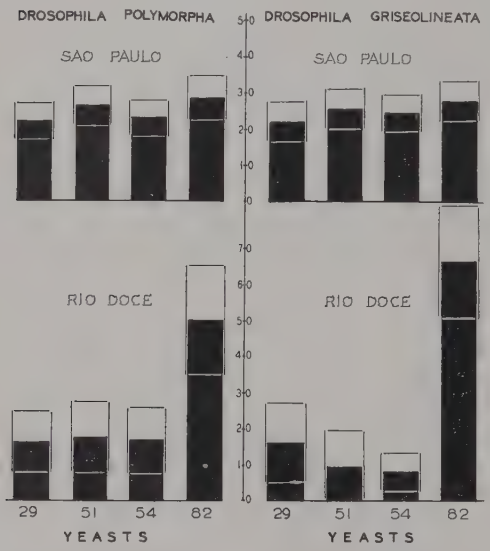

FIG. 1. Proportions of *Drosophila polymorpha* and *D. griseo-lineata* attracted to the different yeasts in different localities. The heights of the columns express the percentages coming to each yeast. The black and white lines at the tops of the columns indicate the limits of two standard deviations from the means.

Drosophila sturtevanti Duda appears to prefer the *Kloeckera* bait (No. 82) on the Rio Doce, at Belem it comes equally to the *Kloeckera* and to one of the *Candida* strains (No. 51), and on the Tapajos it treats the yeasts Nos. 29 and 82 equally. *D. griseolineata* Duda furnished perhaps the clearest instance of racial variation: it visits the four kinds of bait equally at São Paulo but definitely prefers the yeast No. 82 on the Rio Doce (Fig. 1).

The fact that some Drosophila species can distinguish between the three strains of *Candida Krusei* (Nos. 29, 51, 54) which seem to be alike in all standard tests of yeast taxonomy is interesting. Table I suggests such abilities in *D. flavoreapleta* Patterson and Pavan, *D. cardinoides* Dobzhansky and Pavan, *D. calloptera* Schiener, and in some races of *D. sturtevanti* Duda and *D. nebulosa* Sturtevant.

Food Preferences of Sibling Species

The flies entered in Table I under the designation "*willistoni* group" belong to four sibling species, *Drosophila willistoni* Sturtevant, *D. paulistorum* Dobzhansky and Pavan, *D. equinoxialis* Dobzhansky, and *D. tropicalis* Burla and da Cunha. These species are too similar morphologically to permit ready classication under field conditions. Some of the flies were, however, examined cytologically to detect the inversions which many of them carried. The four species are distinguishable by the disc patterns in the chromosomes of their salivary gland cells (Burla *et al.* 1949). Except on the Rio Doce, where *D. willistoni* was by far the commonest species the samples consisted of both *D. willistoni* and *D. paulistorum*. At Belem four individuals of *D. equinoxialis* and three of *D. tropicalis* were also found (not included in Table II). The percentage frequencies of the two species are given in Table II, together with the absolute numbers of the flies tested. In Table II (in contrast to Table I) the percentages indicate the frequencies of *D. willistoni* and *D. paulistorum* among the flies collected on a given yeast, since by no means all the flies of the *willistoni* group that were collected were tested.

One can see that, at Belem, *D. willistoni* was relatively more frequent on the bait fermented with the *Kloeckera* yeast (No. 82), while *D. paulistorum* was relatively more abundant on the No. 54 strain of *Candida*. The Nos. 29 and 51

TABLE II. *Percentages of* Drosophila willistoni *and* D. paulistorum *among the representatives of the* willistoni *species group attracted to different yeasts (the rare species* D. equinoxialis *and* D. tropicalis *disregarded)*

Species & Locality Yeast...	29	51	54	82
Willistoni, Belem	37.5	22.2	11.1	43.0
Paulistorum, Belem	62.5	77.8	88.9	57.0
Flies Classified	72	63	72	72
Willistoni, Tapajos	66.1	66.7	53.8	73.3
Paulistorum, Tapajos	33.9	33.3	46.2	26.7
Flies Classified	56	60	39	60
Willistoni, São Paulo	85.5	89.8	92.6	80.3
Paulistorum, São Paulo	14.5	10.2	7.4	19.7
Flies Classified	69	59	54	71

strains of *Candida* were intermediate. A statistical test for homogeneity gives, for Belem, a chi-square of 25.6, which, for 3 degrees of freedom, is highly significant. On the Tapajos, the figures show the same trend as at Belem (Table II), but here the differences are not statistically significant (chi-square of 3.9). Differences in the food preferences in sibling species, are, thus, clearly indicated.

Conclusions

The experiments reported above made use of only four strains of two species of yeasts. Nevertheless more than half of the species of Drosophila which were collected in appreciable numbers have evinced clear preferences for one or the other of the yeasts (Table I). In some species the preferences are very strong, although no species attended only a single kind of bait. It is impossible to decide whether these preferences are more pronounced in tropical than in temperate species (compare Table I above with the tables in da Cunha, Dobzhansky, and Sokoloff, 1951). More data are obviously needed.

The discovery of racial differences in food preferences is interesting. The evolutionary forces which bring about differentiation of the food preferences evidently work, in at least some instances, on the racial rather than on the specific level. It remains however, to be ascertained whether the yeasts preferred by a given race of Drosospila depend on what other competing species of Drosophila occur in the same region, and on how great a variety of diets are available.

Acknowledgments

The present work was made possible by the cooperation of the Rockefeller Foundation, the National Research Council of Brazil, and "Fundos de Pesquisas da Reitoria da Universidade de São Paulo," which provided grants to defray the costs of the trip to Brazil, and by the generous hospitality of the Director and the Staff of the Instituto Agronomico do Norte, at Belem, Brazil, who permitted the use of the laboratory and other facilities of the Instituto. We are particularly grateful to Dr. G. Addison, F. Camargo, E. Souza Brito, Rubens Lima, J. Murça Pires, and A. L. Froes of the Instituto Agronomico, to Prof. H. J. Phaff of the University of California for the determination of the yeasts, to Miss Sophie Dobzhansky, Mrs. N. Dobzhansky, and Mrs. Lygia da Cunha for their assistance in conducting the experiments.

Summary

Experiments on food preferences of species of Drosophila have been made in four different regions of Brazil: in the equatorial rainforests near Belem and on the lower Tapajos in the State of Pará; on the upper Rio Doce in the State of Minas Geraes; and near the city of São Paulo in Southern Brazil. The flies were attracted to bait consisting of autoclaved banana fermented with one or the other of the four strains of yeasts belong to the species *Candida Krusei* (Nos. 29, 51, and 54 in Table I) or *Kloeckera apiculata* (No. 82).

At least half of the species of Drosophila which were collected in sufficient numbers showed clear preferences for one or the other of the yeast strains (Table I). Some Drosophila species also showed racial variations in food preference (Fig. 1). No species, however, proved rigidly specialized for only one yeast. Some Drosophila species are able to distinguish between strains of yeasts which seem to be identical in standard tests used in yeast systematics.

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THE ECOLOGY AND LIFE HISTORY OF THE POND SNAIL *PHYSA GYRINA*[1]

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Snails form an important part of the fauna of both temporary and permanent ponds. The presence of several species common to both types of habitats indicates the extent to which these animals adapt to extreme environmental conditions. The annual sequence of events in a population of a single species of snail, living in ponds, has not been accurately documented. This paper deals with such a study in the case of *Physa gyrina* Say, a typical inhabitant of temporary and permanent ponds. Populations in three localities were studied; a permanent and a temporary pond in the vicinity of Ann Arbor, Michigan and a permanent pond 300 miles to the north. Periodic collections were made to determine growth and reproduction as limited by various factors in the field and experiments were carried on to obtain information on these aspects under laboratory conditions. In the permanent situations some of the population was active throughout the year, while in the temporary habitat the life cycle was considerably altered by an extended period of dryness. This paper will consider the natural populations studied in the field; the experimental portion will be considered elsewhere.

KENK'S POND, A TEMPORARY HABITAT

The pond studied over a period of two years during this investigation was first described by Kenk (1949) and designated Pond II. It is usually dry by mid-June and fills again in late November. It is located on the west side of U. S. Highway 23 in an open grassy area about five and one-half miles southeast of Ann Arbor, and is bounded on its west side by a low elevation. The north and west margins are bordered by a growth of Typha which extends, in places, as far as five feet out from the shore. A few willows and poplars grow on the northern border. Since 1941, when Kenk studied the pond, the Typha bed has increased considerably in size. The bottom of the pond is covered with a layer of brown, peaty plant remains one to two inches thick underlain by a clay soil.

[1] This material was included in a thesis completed under the direction of Professor F. E. Eggleton and submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, University of Michigan, Ann Arbor.

The gastropod association of Kenk's pond is typical of temporary ponds in this region (Goodrich 1932). The following species, reported by Kenk (1949), were collected there during this investigation:

Lymnaea palustris (Müller)—abundant; *Physa gyrina* Say—abundant; *Helisoma trivolvis* (Say)—common; *Gyraulus parvus* (Say)—common; *Planorbula armigera* (Say)—common.

In addition to the aquatic species, the terrestrial pulmonates, *Deroceras laeve* (Müller) and *Succinea avara* Say, were taken alive in large numbers from beneath the surface of the water in the pond in March, 1951. These land snails are never typical of such situations during the summer and were collected here after the ice cover had disappeared at which time the water temperature was 7° C.

SCIO POND, A PERMANENT HABITAT

Located about eight and one-half miles northwest of Ann Arbor on Zeeb Road near the Huron River Drive, the pond is a remnant of an old artificial channel of the river. During late fall and spring, it is of maximum size—approximately 150 feet long and 30 feet wide, the deepest portion being about 4 feet. From late July to early October, at low water, a shallow area extending across the pond from north to south is exposed, thus separating the habitat into two portions; one, at the western end, no longer in direct communication with the river, and an eastern part into which river water still freely passes. The isolated portion is about 12 by 20 feet and one foot in depth during the driest period of the year.

The pond is densely shaded by a large number of elms and willows mixed with a few maples. In contrast to Kenk's pond, no Typha is present nor is that part of the bottom exposed during the dry season invaded by herbaceous plants. A sparse growth of Sagittaria occurs in both portions. By far the most abaundant aquatic vegetation is filamentous algae, which grows in large masses. The bottom of the western portion is thickly covered with leaves under which lies a layer of black muck mixed with brown, peaty material. The bottom of the eastern portion, subjected to action of river currents, is relatively free from accumulated plant debris and consists of

muddy sand, coarse gravel, cobble stones and boulders. The population is confined largely to the western, more sheltered portion where the water is relatively quiet and a more abundant supply of food is present.

The gastropod fauna is quite different from the association found in a temporary pond. Both typical river forms and those associated with backwaters are found here.

The Streptoneura found were *Campeloma decisum* (Say)—abundant; *Valvata tricarinata* (Say)—common; *Amnicola limosa* (Say)—common; and *Amnicola lustrica* Pilsbry—common. Pulmonata found were *Lymnaea palustris* (Müller)—common; *Lymnaea obrussa* Say—abundant; *Lymnaea humilis* Say—common; *Physa gyrina* Say—abundant; *Helisoma trivolvis* (Say)—common; *Planorbula armigera* (Say)—common; and *Ferrissia rivularis* (Say)—rare.

Operculate snails are not found in temporary waters. The fact that this group, present in the western portion of the pond isolated from direct contact with the river from late July until early October, can maintain itself, is due to seepage from the river into this area.

In a river, *Campeloma* is ordinarily present in largest numbers along reaches where, due to slow moving currents, silt has been rather heavily deposited. The particular habitat at Scio meets these requirements and a large population has established itself.

The presence of two species of *Amnicola* is not unusual. They are tolerant of a wide range of natural habitats being found in creeks, rivers, and fresh- and brackish-water lakes (Berry 1943). *Valvata* has also been reported from a diversity of habitats (Baker 1928) and during this investigation has been encountered in a variety of waters.

Although the Scio habitat is more or less permanent, it possesses many of the features of a temporary pond. *L. palustris, P. gyrina, H. trivolvis* and *P. armigera* are ordinarily found together in temporary waters and *L. obrussa* and *L. humilis* are frequently found in association with them. Temporariness of habitat is certainly not a requisite for completion of the life cycle of these snails, rather it is a factor to which they have successfully adapted.

The typical stream form, *Ferrissia,* is not well established in the pool and its presence is probably accidental.

With reduction of temperature in the fall a third assemblage of species, the terrestrial pulmonates, makes its appearance. *Deroceras laeve* has consistently been present in winter collections from temporary and permanent ponds. These slugs are able to survive several months' submergence. Pearl (1902) reports that this slug crawls into water as the temperature drops and leaves it as temperatures rise. These facts indicate that this is probably a part of the normal behavior in certain slugs. Other terrestrial species, *Succinea* and *Zonitoides,* have been recovered from similar situations.

Life Cycle

Kenk's Pond

Physa gyrina began to oviposit in April when the temperature of the water had risen to at least 10° C.; the eggs hatched in from eight to ten days. Juveniles fed continuously and as the pond began to dry moved toward the center where water remained longest. Before all standing water had disappeared, the immature snails burrowed into the relatively soft bottom and remained there until the fall rains filled the pond. Then the snails came out of the bottom deposits and began to move about and feed. As the water temperature lowered during the fall, the snails were increasingly less active. During the winter they moved very slowly under the ice or remained motionless for long periods of time. Some growth must have occurred during the winter months because mature snails which were scarce in the fall, predominated in spring collections.

The fact that the pond is, at times, without water during the winter months is probably a major factor in reducing the size of the population. Kenk reported such a case during the winter of 1944-45. Again, in the winter of 1950-51 standing water was not present until late January. Although *P. gyrina* were present in March of 1951 they were less abundant than in the preceding year when the pond was filled in November.

Scio Pond

Field observations and collections of *P. gyrina* were made in the western portion of the pond. Although subject to the greatest fluctuations of water level, this area supported the largest numbers of these snails. While the water temperature ranged from 1.5 to 3° C. the population was concentrated in deeper (3-4 feet) water. As the temperature rose, the snails moved to shallower (2-6 inches) portions of the pond.

As in Kenk's pond, temperature appears to be the factor controlling oviposition. In April, when the water temperature was above 10° C., the population consisted almost entirely of sexually mature individuals which began to oviposit. In May the adult population had been virtually replaced by juveniles. Egg masses were relatively scarce.

Throughout the remaining warm months (June through October) no snails were observed in copulation and no egg masses were found in the field. From August on the population contained a high percentage of individuals within the size range of snails which oviposited in the spring. Some of those collected in August and succeeding months laid eggs when brought into the laboratory. These were snails born in the spring which were sexually mature by late summer or early fall of that year. The second generation they produced did not mature until after May of the following year. This accounts for the few juveniles present in the population following May and the few adults observed in May.

Neither laboratory raised nor field collected snails from Scio oviposited before reaching 7 mm in length. Observations made on 60 snails indicates that length is the most reliable index of sexual maturity. All snails (from the Scio population) 7 mm or over are considered to be capable of ovipositing under favorable environmental conditions. Relative proportions of sexually immature and mature *P. gyrina* over a complete annual cycle are given in Figure 1.

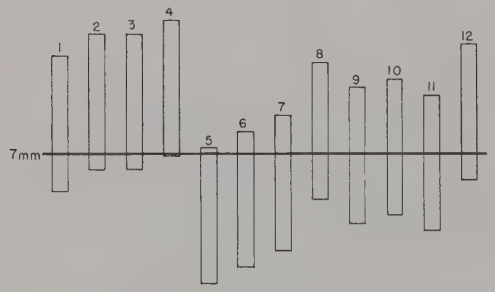

FIG. 1. Per cent of sexually immature and mature *Physa gyrina* within each month's collection from Scio. The numbers refer to the month in which the collection was made.

Most of the parent generation died during the month of April following a burst of oviposition. In May the population was composed almost exclusively of newly hatched individuals measuring from one to three mm in length. Various combinations of factors contributed to the disappearance of uniformity within the population during the succeeding months (Fig. 2). Early growth is so rapid (DeWitt *in press*) that age differences between broods laid by a single parent may be prominent and the effect of differential growth rates together with localized environmental inhibitors and stimuli contribute to this heterogeneity. In addition, a small number of ovipositing individuals were present in May and June. From November to April oviposition ceased and although growth was retarded by low temperature there was a general increase in the mean size of the population.

Black River Pond

This pond, a backwater of the Black River, is located in Cheboygan County about 300 miles north of Ann Arbor. In most respects it resembles the Scio locality. It was visited in mid-May and a collection of mature *P. gyrina* was made. At this time, large numbers of egg masses were present on submerged vegetation and many snails were in copulation.

One month later the population had changed radically; juveniles predominated, only a few individuals of adult size were taken. No egg masses were found. Subsequent visits during the months of June, July and August yielded a series of *P. gyrina* which showed an increase in mean size each month.

DISCUSSION

Under relatively stable laboratory conditions, *Physa gyrina* may live as long as 22 months. There is no indication that a rest period is essential to growth or activity. Laboratory-reared snails successively undergo developmental, reproductive and post-reproductive periods and are not subjected to such fluctuating environmental factors as temperature, desiccation, parasitism, anaerobiosis and food supply, as they would be in a natural habitat. In permanent ponds, the life cycle extends over 12 to 13 months while those populations in temporary ponds may live for an additional six months.

None of the snails living in temporary ponds are restricted to these habitats but have developed a tolerance to limited desiccation. Survival in such an environment may be accomplished in several ways. Baker (1914) thought that failure to find living snails during dry periods indicated that the egg masses were resistant to desiccation. In Kenk's pond, however, immature *P. gyrina* were estivating in dry bottom materials. Mozley (1932) reported that *Lymnaea palustris* formed an epiphragm during the dry season; such a structure was not observed in any *P. gyrina*. From my observations it appears that immature snails, perhaps because of area of exposed surface, are more resistant to drought than are adults. Cheatum (1934) demonstrated that the resistance of temporary pond species to desiccation is greater than that of lake pulmonates. Estivation forced upon *P. gyrina* in temporary ponds delays growth and the snails hatching in the spring rarely at-

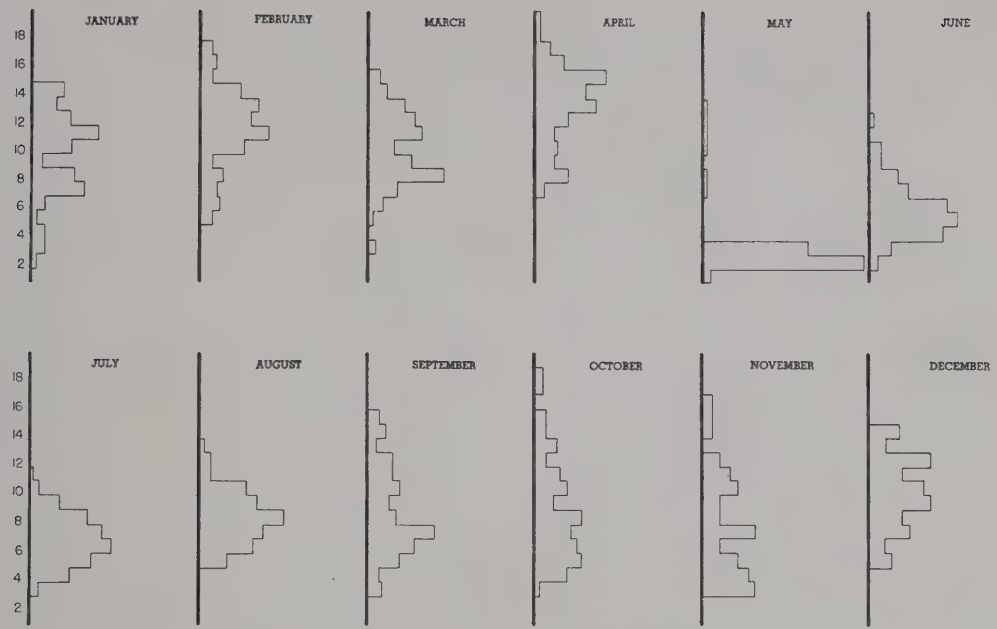

FIG. 2. Monthly collections of *Physa gyrina* from Scio plotted according to the percentage of individuals falling within certain size-class limits. The numbers represent the length of the shell in millimeters.

tain sexual maturity by the fall of the same year as do individuals living in permanent ponds. The length of the dry season can alter the life cycle. If long enough, there is not enough time in the spring for the animals to become sexually mature and they may overwinter a second year.

In both habitats, temperature is the critical factor controlling overt reproductive behavior. Copulation and oviposition do not take place until the water temperature has reached 10 to 12° C. Although sexually mature individuals were very common in Scio pond from early fall through winter, large numbers of egg masses were not present until spring. A few individuals born in the spring did become sexually mature by late summer and these oviposited as long as the temperature remained at or above the critical point. Sexually mature snails were present in Kenk's pond only in the spring. This temperature-controlled reproductive pattern is not present in laboratory reared snails. They begin to oviposit at the end of the developmental period regardless of the season. Similar conditions were approximated in a stream in Illinois fed by warm waste waters in which *P. gyrina* lived and oviposited continuously irrespective of air temperatures (Agersborg 1932).

Severe anaerobic conditions may result in death of a large number of individuals within a population but such conditions are probably more frequently encountered in temporary than in permanent waters. It has been demonstrated experimentally that *P. gyrina* possesses a limited anaerobic resistance (Von Brand, Baernstein, and Mehlman 1950) and I have taken these snails alive from bottom deposits in temporary ponds when hydrogen sulfide was so abundant that its odor was detected as soon as the ice cover had been broken. The water immediately under the ice contained 3.2 ppm of free oxygen but this quantity would steadily decrease as the bottom of the pond was approached. These conditions exist only when ice covers the ponds and Alsterberg (1930) has shown that snails kept anaerobically at from 0 to 10° C. live three times as long as those kept at 20°. In addition, chemical and physical factors are so varied within a given habitat, that snails, which are capable of moving from one microhabitat to another, quite possibly do not have to undergo an extended absence of free oxygen.

Most of the food supply in temporary ponds is derived from terrestrial plants; permanent ponds are likely to support a flora of aquatic flowering plants which supplements the other sources of food. The diet of *P. gyrina* consists of dead and decaying vegetation together with living algae and water molds. Animal remains, although eaten when available, constitute a minor portion of the diet. A liberal supply of organic matter in the

form of dead leaves is present in those ponds found in a wooded area; those in more open regions frequently have a portion of their margins bordered with Typha whose leaves when dead and submerged form a favorable substrate for a growth of algae and water molds. In addition, grasses and other herbaceous plants invade the bottom of temporary ponds during the dry season and furnish quantities of dead plant material when the ponds become filled.

Death within a field population can be attributed to a variety of causes. The species has a maximum life expectancy which depends upon its genetic constitution and the limitations of the environment. Since *Physa gyrina* is monoecious, a differential death rate, which is a factor in determining composition of some populations, can be disregarded. Accidental death, due to deviations from optimal ecological conditions such as pollution, and to scarcity of food, did not appear to play a significant role within any of the populations studied.

Species in temporary ponds, incapable of leaving such an environment, are subjected to factors causing high mortality within the population. These habitats are highly selective and species living here are likely to become genetically homogeneous at a more rapid rate than those which can migrate or which live in a less rigorous habitat.

Summary

Physa gyrina is a typical inhabitant of temporary and permanent ponds. The life history and ecology of this pulmonate snail were studied in three ponds in Michigan. In a permanent pond in southern Michigan, oviposition occurred in the spring when water temperatures reached 10 to 12° C. The adult population died shortly thereafter. Snails born in the spring may reach sexual maturity that fall, but most oviposition is delayed by low temperatures until the following spring. Within the Scio population a shell length of seven mm was determined to be the size below which snails are believed to be sexually immature. Those individuals seven or more millimeters in length are capable of ovipositing under favorable environmental conditions. The life span of individuals in the field is from twelve to thirteen months. The life history of *P. gyrina* in a permanent pond 300 miles north of the above-mentioned habitat differed only in that oviposition took place three to four weeks later in the spring.

Temporary ponds, located in southern Michigan, are usually dry from mid-June until November. Estivation forced upon *P. gyrina* living in such habitats delays growth, and the snails rarely attain sexual maturity by the fall of the year in which they hatch. The time to reach maturity the following spring is dependent upon the length of estivation. If the dry period is unusually long, the snails may overwinter a second year. Thus the life span in such situations may be considerably longer than in permanent ponds.

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PHYTOSOCIOLOGY OF CORTICOLOUS CRYPTOGAMS IN THE UPLAND FORESTS OF SOUTHERN WISCONSIN

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INTRODUCTION

The phytosociology of corticolous cryptogams (lichens and bryophytes) has been primarily a qualitative descriptive science. If quantitative methods are used, they are often applied in a subjective manner so that the results are not always trustworthy and may not usually be treated statistically. The following investigation was undertaken in part to illustrate the applicability of statistical analysis to the cryptogamic vegetation in the upland forests of southern Wisconsin. The principal objectives were to obtain an adequate sample of the stands of tree vegetation and of the tree species in the region and to sample the cryptogamic vegetation on the individual trees. With these basic field data, it was possible to analyze objectively the following specific problems:

1. Correlation of the cryptogamic vegetation of various stands with changes in stand composition and environment.
2. Analysis of the cryptogamic vegetation of the individual tree species in order to evaluate the relative effect of host specificity.
3. The interrelations of the cryptogams and their biological similarity as determined by interspecific association and an interpretation of community structure.

DESCRIPTION OF THE AREA

This study was carried out in the upland forest province of southern Wisconsin, north-central United States. There are 27 counties in this region with an aggregate area of about 15,000 square miles. The following generalized description of the vegetation is taken from Curtis and McIntosh (1951):

"The southern half of Wisconsin lies in the broad ecotonal belt between grassland and summergreen forest. . . . The present-day stands of natural vegetation are mostly derived from [oak openings and broadleaf deciduous forests]. The deciduous forests occur on a range of topographic sites, from very dry through mesic to very wet. The driest sites, on cliffs, sandy soil and southwest slopes, are characteristically covered with scattered stands of small oaks (*Quercus macrocarpa, Q. velutina*). As moisture conditions improve, the forests become more dense with a greater number of important tree species. The most mesic conditions commonly support sugar maple, basswood, or other species of similar requirements." The present stands exist as isolated wood lots of 15 to over 300 acres, set off from the surrounding vegetation by ploughed fields which occupy the greater portion of this highly agricultural region.

The western half of the prairie-forest border, situated in the Driftless Area, is characterized in certain parts by mature dissected topography, although much of it, especially where stands are located, is subdued and rolling. The eastern half of the state has been glaciated and is rolling to flat. The climate of the area is intermediate between that of a forested region and that of the prairie (Borchert 1950).

METHODS

TREE VEGETATION

When the present study was initiated, a large number of stand samples of the upland forests had already been located and analyzed (Curtis and McIntosh 1951). The selection of these stands was based on criteria which effectively limited subjective decisions as to their suitability. Any undisturbed stand of natural vegetation more than 15 acres in size was selected regardless of the tree composition. After a stand was located in the present study, the tree components were sampled with the random pairs method of forest ecology (Cottam and Curtis 1949). This method is rapidly applied in the field by a lone worker. Twenty points (40 trees) were sampled when it was discovered that the results from this sample approximated those from a standard 80 tree sample with an average deviation of less than ± 5 per cent. The time required for a careful examination of the cryptogams on the individual trees imposed the need for the smaller sample. Transects were taken in the central 5 acre portion of each stand where peripheral phenomena, such as edge lighting, wind, and road dust, were presumably at a minimum.

[1] This work was supported in part by a grant from the Wisconsin Alumni Research Foundation. I wish to thank J. T. Curtis, J. W. Thomson, F. Gruenberger, G. Cottam, H. S. Conard, and W. C. Steere for aid during the course of the project.

The above method differs rather significantly from commonly accepted methods employed by cryptogamists in that the trees were not first selected on the basis of their cryptogamic vegetation. Indeed, 10 per cent of the trees sampled in the prairie-forest border had no cryptogams at all at 1.3 m. By using comparable methods, moreover, a later worker can repeat a survey of the same stand and expect to obtain the same basic data, within the limits of sampling error, even though subsequent analysis and interpretation of the results may differ.

CRYPTOGAMIC VEGETATION

It is known that epiphytes form a gradient of communities along tree trunks, each reaching optimal development at some level from base to canopy (*cf.* Hale 1952). Complete examination of many trees in the prairie-forest border would have been so impractical and time-consuming that the highest level to be investigated was set at about 1.3 m. Since there is, in addition, a fairly obvious demarcation in the floristics and physiognomy of the cryptogamic vegetation at the base of trees as opposed to the area at 1.3 m. height, it was decided that these two levels should be treated separately throughout the study. At 1.3 m., where lichens dominate, cryptogams were recorded from a vertical area 40 cm. high, a kind of cylindrical quadrat centered at 1.3 m. and girdling the trunk. This is in reality a nearly complete sample of the vegetation at 1.3 m. At the base, where bryophytes normally form a rather continuous mat 10-30 or 40 cm. high, the species were examined from ground level to 30 cm. along the trunk. As a rule, tree bases in the prairie-forest border are not slanting nor are there any exposed roots above ground.

The only information about the cryptogams obtained in this investigation is whether a particular species was on a given tree or not regardless of its coverage, a decision which could be made very quickly. This species-presence method, so well adapted to mass sampling, furnishes an exceedingly valuable framework around which future more detailed studies can be made. After a reconnaissance of several stands to determine what cryptogams might be encountered, field data sheets were prepared in order to facilitate rapid collection of data from a large number of individual trees; 2797 were actually tallied. Tree species and d.b.h. (1.3 m.) were recorded for 40 trees per stand and the cryptogams on each tree indicated merely by checks. Two measurements of the crytogams are provided by this method. One is the occurrence of species in various groups of stands, a synthetic character hereafter termed *constancy,* calculated by dividing the number of stands in which a cryptogam was found at least once by the total number of stands. Constancy is a good quantitative measure of the broad range of a species. Another type of information concerns the distribution of cryptogams on the individual trees within each stand or group of stands. It is best called *frequency,* equalling the number of trees on which a cryptogam was collected divided by the total number of trees. Frequency indicates the relative dispersion of cryptogams on the trees and affords a statistical measure of the probability of finding a species in a random sample of trees.

The basic field data were accumulated in such quantities that special techniques had to be employed to analyze them. All information was summarized on appropriate sheets and in addition the individual tree data were reproduced on 2797 IBM punch cards (Hale 1953). The paramount advantage of IBM methods lies in the resulting flexibility of the data and in the rapid means available for analyzing them. Many of the

TABLE I. *Frequency on 2797 trees and constancy in 72 stands of the 30 cryptogams with a frequency of more than 5% at 1.3 m. or base in the upland forests. All percentages in this paper are carried to the nearest unit*

	Frequency		Constancy	
	1.3 m.	Base	1.3 m.	Base
Allarthonia caesia	40	27	95	93
Candelaria concolor	26	6	81	39
Frullania eboracensis	28	23	86	93
Graphis scripta	32	24	86	83
Lecanora subfuscata	12	1	57	20
Lindbergia austinii	13	2	68	45
Opegrapha pulicaris	6	2	49	31
Orthotrichum pumilum	7	1	61	26
Parmelia aurulenta	30	21	81	72
Parmelia borreri	11	2	58	11
Parmelia caperata	17	7	63	35
Parmelia rudecta	34	19	86	77
Physcia aipolia	22	2	83	18
Physcia elaeina	5	1	50	25
Physcia grisea	19	7	70	45
Physcia millegrana	31	9	83	53
Physcia tribacoides	12	2	61	25
Xanthoria fallax	6	1	50	17
Amblystegium varium	1	18	1	95
Anomodon attenuatus	—	6	—	50
Anomodon minor	3	18	38	85
Chamberlainia acuminata	1	35	4	95
Cladonia coniocraea	1	13	17	63
Entodon sp.	1	26	1	81
cf. Lecanora symmicta	12	33	75	90
Lepraria aeruginosa	15	25	68	79
Leskea polycarpa	1	11	10	79
Mnium cuspidatum	1	47	3	95
Physcia orbicularis	51	64	97	100
Platygyrium repens	29	52	93	100

analyses to be presented in fact would have been impossible without recourse to IBM.

Results

Floristics of the Cryptogams

In this investigation, 88 species of cryptogams, including 33 bryophytes and 55 lichens, were collected and identified. Representative specimens of all cryptogams mentioned in the study were deposited in the herbarium of the University of Wisconsin. Two new species of *Rinodina, R. halei* and *R. papillata,* were described by Magnusson (1953) from material sent him.

The cryptogams which have a frequency of more than 5 per cent on the 2797 trees are listed in Table I where frequency and constancy at both 1.3 m. and base are given. The rarer species of less than 5 per cent frequency are listed below:

More frequent at 1.3 m.:

Anaptychia hypoleuca
Arthonia radiata
Arthopyrenia finkii
Buellia stillingiana
Caloplaca aurantiaca
Candelaria fibrosa
Candelariella vitellina
Parmelia crinita
P. subaurifera
P. subquercifolia
P. sulcata
P. trichotera
Pertusaria multipuncta
P. pustulata
P. pertusa
P. velata
Physcia ciliata
P. stellaris
P. syncolla
Pylaisia selwynii
Pyrenula nitida
Pyxine sorediata
Ramalina fastigiata
Rinodina halei
R. papillata

More frequent at base:

Anaptychia speciosa
Anomodon rostratus
Bacidia spp.
Brachythecium sp.
Bryum capillare
Caloplaca microphyllina
Campylium hispidulum
Ceratodon purpureus
Cladonia chlorophaea (group)
C. pyxidata
Collema sp.
Dicranum montanum
Eurrhynchium serrulatum
Fissidens subbasilaris
Homomallium adnatum
Hypnum reptile
Lecanora varia
Lophocolea heterophylla
Parmelia conspersa isidiata
Peltigera canina rufescens
P. polydactyla
Pertusaria amara
Physcia pulverulenta
Plagiothecium deplanatum
Polytrichum piliferum
Porella platyphylla
Ptilidium pulcherrimum
Rhodobryum roseum
Thelia asprella
Thuidium delicatulum
T. minutulum
Tortella humilis
Ulota crispa

All of the bryophytes had previously been reported from Wisconsin (Cheney and Evans 1944); nomenclature follows Steere (1947). The nomenclature of the lichens follows Fink (1935) with cerain modifications given by Hale (1950). Several bryophytes had to be grouped since the overwhelming frequency of sterile or juvenile plants prevented critical identification. *Brachythecium* sp. includes at least *B. oxycladon* and *B. salebrosum. Entodon* sp. covers *E. cladorrhizans,* apparently the most common species, *E. compressus,* and *E. seductrix.* Cf. *Lecanora symmicta* is an unknown sterile crustose lichen. Quantitative collections of most pyrenocarpous lichens were not made since they were so difficult to detect in the field and to identify.

The Tree Vegetation

Since an adequate study of the tree vegetation was prerequisite to an analysis of the cryptogamic vegetation, the author in effect repeated the previous survey of the southern upland hardwoods. The object of this intensive study of the tree vegetation was chiefly to make possible detailed analyses of the variations of cryptogamic vegetation in stands of different tree composition and also to supply a large random sample of the various tree species. In all, 72 stands of upland vegetation, evenly distributed over the prairie-forest border, were located and sampled (Fig. 1).

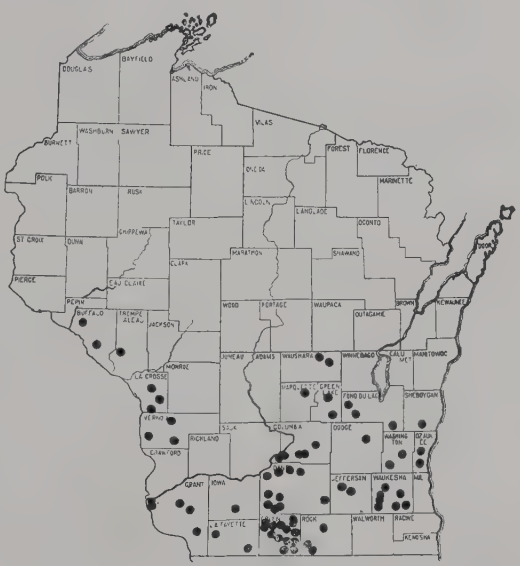

Fig. 1. Map of the state of Wisconsin showing the locations of 72 stands of upland hardwoods in the prairie-forest border. The greatest dimension of the region is about 250 miles.

Floristically the tree data are similar to those presented earlier by Curtis and McIntosh (1951). The major tree group is *Quercus rubra-Q. velutina* with *Q. alba* and *Acer saccharum* the next most common (Table II). These trees have considerably higher importance than the remaining ones. It will be noted that conifers are absent from normal upland sites.

The 72 stands as components of the vegetation cannot be analysed separately because of their

TABLE II. *Tree species encountered in the upland forests with total number of individuals in this study and the climax adaptation number, the latter value from Curtis and McIntosh (1951)*

	Number of individuals	Climax adaptation no.
Quercus alba	644	4
Quercus rubra	507	6
Acer saccharum	373	10
Quercus velutina	311	2
Tilia americana	189	7
Ulmus rubra	136	8
Carya ovata	125	3.5
Ostrya virginiana	88	9
Quercus macrocarpa	85	1
Prunus serotina	72	3.5
Fagus grandifolia	61	10
Fraxinus americana	54	7.5
Ulmus americana	36	4
Carya cordiformis	34	8.5
Juglans nigra	31	5
Acer rubrum	20	7
Juglans cinerea	16	7
Populus sp.	11	1
Celtis occidentalis	3	8
Carpinus caroliniana	1	8

numerical bulk, but must be arranged along some gradient or placed into groups with similar features so that averaged conditions of like stands may be compared. In a mass sample problem, it is usually thus necessary to divert attention from descriptions of individual stands. A satisfactory technique of assembling stand data is that proposed by Curtis and McIntosh (1951). In this relatively simple procedure, the percentage density, per cent sum of frequency, and percentage dominance of each tree are first totaled separately to produce the so-called importance value. This value is multiplied by the climax adaptation number of that tree (Table II). The climax adaptation number expresses the autecological position of the tree relative to *Quercus macrocarpa* (1), a tree most frequent in pioneer sites, and *Acer saccharum* (10), the most common tree of climax vegetation. The final summation of the weighted importance values for all trees in a stand gives the vegetational continuum index which is then used to locate the stand on a linear gradient of index values ranging from 300 to 3000. Wherever stands of the original survey were repeated, the values agreed very closely, even though the stand sample was only half as large here. The relative density of each tree by stand was plotted against the continuum index (Fig. 2) in order to show the quantitative relations of the species. These curves resemble the original data for importance value versus continuum index (Curtis and McIntosh 1951). Density is used here since the number of individuals of each tree per stand is

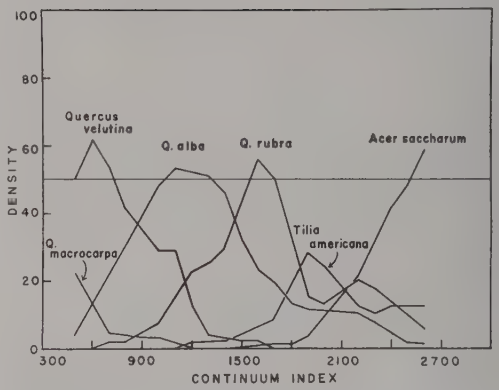

FIG. 2. Stand density of 6 major trees in order of continuum index. Lines connect the average value of density per 100 unit continuum interval, smoothed with the formula $(a + 2b + c)/4$.

the most valuable information in a cryptogamic study.

Stands with a continuum index below 600 in this study are classifiable as *oak openings*. Two trees are common as dominants, *Quercus macrocarpa* and *Q. velutina*. Few undisturbed stands of this type are to be found at present because they are so often utilized for grazing. The low understory is composed mainly of grasses and forbs. These oak openings represent the most pioneer forest community in the prairie-forest border.

The stands above continuum index 600 invariably have a closed canopy and a shrubby understory with an increase in the number of tree species. There are roughly three types of stands in the interval 600 to 1800 index, the *oak woods*. From 600-900 *Quercus velutina* is often the dominant with *Q. alba* as a common associate. Minor trees include *Carya ovata, Prunus serotina,* and *Q. macrocarpa*. A large group of stands from 900-1400 index usually contain *Q. alba* (Fig. 3) with *Q. rubra* and *Q. velutina* and their hybrids and *Carya ovata* and *Prunus serotina* as lesser trees. The shrub layer is not dense and rarely obscures the trunks. Stands from 1400-1800 index contain *Q. ruba* as the dominant with *Q. alba, Carya ovata,* and *Prunus serotina* having lesser importance. All three types of oak woods encountered in this study have rather similar appearance in the field with moderate understory and fairly uniform light conditions. They have broad distribution in the prairie-forest border and probably make up more than one-half of the vegetation cover, reaching greatest frequency however in the western half of the state.

Stands above 1800 continuum index represent

FIG. 3. Fall aspect of an oak woods dominated by *Quercus alba*. Note the sharply defined basal moss layer.

the climax vegetation of the prairie-forest border. The shrub layer is relatively unimportant and the trees of the oak woods play a minor role. From 1800 to about 2200 there were only four stands in this study, all dominated by *Tilia americana*. This interval is apparently a rare transitory stage which comprises a very small part of the present-day vegetation. Above 2200, *Acer saccharum* and related climax species, *Ostrya virginiana, Tilia americana,* and *Ulmus rubra,* make up the bulk of the vegetation. The stands, appropriately called the *maple woods,* account for the second most abundant type of forest cover in the region; they occur with greatest frequency in the eastern half of the state. In addition, three stands containing *Fagus grandifolia,* a tree often ecologically similar to *Acer saccharum,* were sampled.

Although the continuum is a gradient of tree species, environmental factors are known to correlate with it. Curtis and McIntosh (1951) found for instance that various soil characters correlate with the present order of stands. The author investigated several factors which might be expected to limit the distribution of cryptogams. It was discovered that stands below 600 continuum index, the oak openings, receive more than 10 per cent full sunlight at 1.3 m. on the trunks in summer. Stands in the oak woods receive on the average 3-6 per cent full sunlight, approximately 10 times the amount received at 1.3 m. in climax maple woods. These outstanding differences in light relations along the continuum gradient are undoubtedly paralleled by other meteorological parameters, such as vapor pressure deficit, temperature, and wind.

THE CRYPTOGAMIC VEGETATION

Analysis of the cryptogamic vegetation will be carried out from two separate points of view. In the first approach, it is possible to study the frequency behavior of cryptogams along a gradient of stands. This method emphasizes the position of cryptogams as components of the forest community and can afford an objective means of correlating variations in their frequency with forest composition and environment. In a second type of analysis, the cryptogamic vegetation of the various tree species, considered apart from their role as stand components, will be examined and compared with due regard to the quantitative features of this problem.

Distribution of cryptogams along the continuum

The continuum index was conceived as a basic "framework upon which a great amount of independently derived information may be arranged and interrelated" (Curtis and McIntosh 1951). It would be advantageous to analyse the frequency behavior of the cryptogams in the upland forests along the continuum gradient erected previously for the tree vegetation. The 72 stands were initially arranged in order of continuum index and the individual stand frequencies plotted; a resulting scatter diagram for *Parmelia aurulenta* at 1.3 m. is shown in Figure 4. The scattering of points is an expected phenomenon when one deals with many samples of a large variable population. These diagrams are difficult to analyse until the trend of the points is expressed as a curve. The values for each 100 unit continuum interval were therefore averaged by dividing the sum of frequency by the total number of stands in the interval, whether or not a stand had the cryptogam. The resulting curve is also shown in Figure 4. This statistical treatment stresses the average frequency of a cryptogam and never involves discussion of a single statistic, the stand.

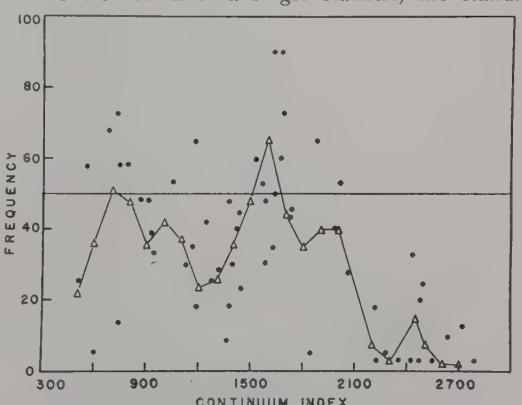

FIG. 4. Stand frequencies (dots) of *Parmelia aurulenta* at 1. 3 m. arranged in order of continuum index. Triangles represent the 100 unit continuum interval averages.

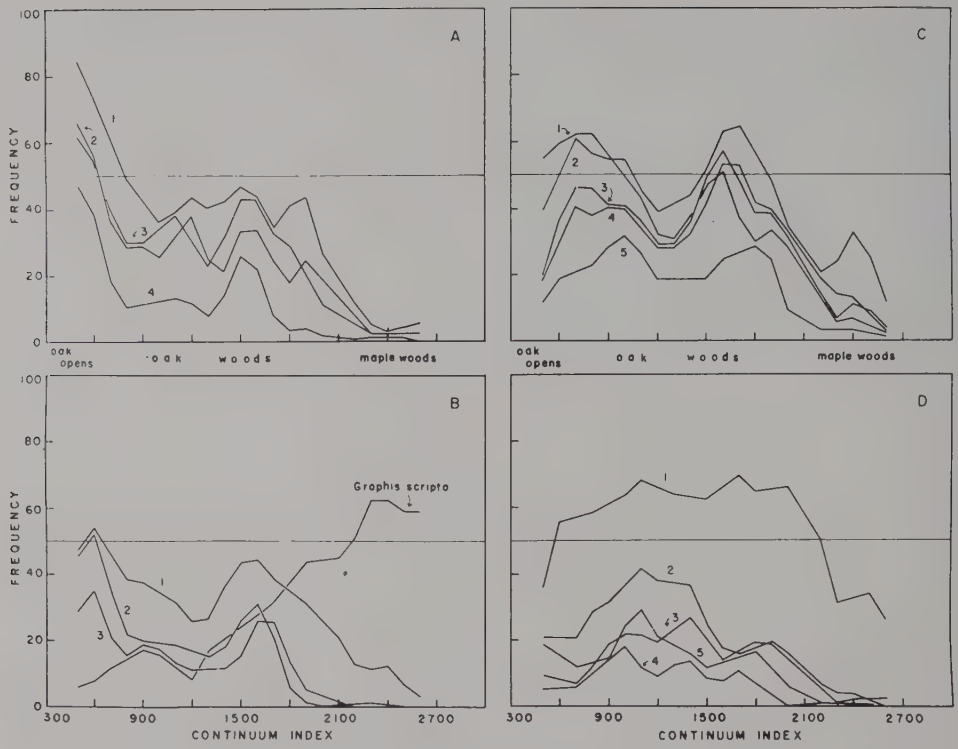

FIG. 5 A-D. Stand frequencies of major cryptogams at 1.3 m. arranged in order of continuum index. Lines as in Fig. 2.

5A: 1, *Physcia millegrana;* 2, *Parmelia caperata;* 3,*Candelaria concolor;* 4, *Parmelia borreri.*

5B: 1, *Frullania eboracensis;* 2, *Parmelia caperata;* 3, *Lecanora subfuscata.*

5C: 1, *Parmelia rudecta*; 2, *Allarthonia caesia;* 3, *Parmelia aurulenta;* 4, *Platygyrium repens;* 5, *Lepraria aeruginosa.*

5D: 1, *Physcia orbicularis;* 2, *P. grisea;* 3, *Lindbergia austinii;* 4, *Opegrapha pulicaris;* 5, *P. tribacoides.*

Analysis of cryptogams at 1.3 m.—Although all cryptogams were plotted along the continuum gradient, only species of more than 5-10 per cent frequency on the 2797 trees formed definable averaged curves which could be analyzed. After a preliminary examination of the graphs, it became apparent that many of the species formed curves which bore strong superficial resemblance. Such curves will be plotted together in order to condense the data.

At 1.3 m., all cryptogams that were graphed, with the exception of *Graphis scripta,* attain maximum frequency in the oak openings or oak woods and drop to low frequency in the maple woods (Fig. 5). *G. scripta* has a sharp peak of frequency in the maple woods but loses importance rapidly in the oak woods (Fig. 5B). This lichen and apparently the rare *Arthonia radiata* are the only cryptogams at 1.3 m. which are characteristic of climax trees.

Cryptogams in the oak-dominated stands (300-1800 index) are by no means all alike in behavior. There is one well-defined group with much higher frequency in the pioneer oak openings than in the more mesic oak woods. This includes in particular:

Candelaria concolor	*Physcia aipolia*
Parmelia borreri	*P. millegrana.*

These species are summarized graphically in Fig. 5A. It is known from extensive field observation and unpublished field data that these species form a conspicuous element in the cryptogamic vegetation of isolated trees and cedar glades. It would appear that the upland forests within the limits of this investigation do not offer an environment suitable to the optimal development and full range of these species. They maintain a moderate though irregular level of frequency in the

oak woods, then disappear or drop to very low frequency in maple woods.

The following species, which have optimal ranges within the upland hardwoods, may be combined into a second major group:

Allarthonia caesia — *P. rudecta*
Lepraria aeruginosa — *Platygyrium repens*
Parmelia aurulenta

They have distinctly bimodal curves of distribution (Fig. 5C) with both rather broad peaks of about the same size, coinciding it would seem with the optimal ranges of *Quercus rubra* and *Q. velutina*. The peaks drop sharply both in oak openings and in the maple woods. Many rarer species, such as *Buellia stillingiana, Ramalina fastigiata,* and *Rinodina papillata,* have more or less identical bimodal distributions.

A third and smaller grouping includes *Frullania eboracensis, Lecanora subfuscata,* and *Parmelia caperata* (Fig. 5B). They are somewhat more abundant in oak openings and seem intermediate between the former two groups.

Another set of species (Fig. 5D) with unimodal distributions also attain maximum frequency within the upland hardwoods. One of them, *Physcia orbicularis* (Fig. 5D) has a very high frequency and an enormous range over the entire continuum. The remaining four,

Lindbergia austinii — *Physcia grisea*
Opegrapha pulicaris — *P. tribacoides*

peak in the interval 900-1400, the *Quercus alba* woods, between the peaks of the bimodal species. It is probable that rarer *Orthotrichum pumilum, Physcia ciliata* and *P. elaeina, Pylaisia selwynii,* and *Xanthoria fallax* belong with this group.

The remaining species cannot be easily categorized with any of the above provisional groups. Cf. *Lecanora symmicta,* for example, has a very broad amplitude but low frequency. Other minor species show no graphical peaks; most however have maximum frequency and constancy in the oak woods.

Analysis of cryptogams at base.—Cryptogams which have definable curves of frequency at bases of trees include many species already discussed at 1.3 m. in addition to species not found above base with significant frequency. The first group (Fig. 6A), beginning with those of maximum frequency in oak openings, includes

Cladonia coniocraea — *Parmelia caperata*
Parmelia rudecta — *Physcia millegrana.*
Candelaria concolor

The latter three species drop very rapidly to a low frequency level in the oak woods while the first two retain moderate frequency there. *Physcia aipolia, Parmelia borreri,* and *Lecanora subfuscata* appear to have distribution similar to the latter three although they are exceedingly rare at base.

Species with bimodal distributions which have low frequency in oak openings and maple woods include (Fig. 6B)

Allarthonia caesia — *Lepraria aeruginosa*
Entodon sp. — *Parmelia aurulenta.*
Frullania eboracensis

In general, the frequency behavior of the cryptogams along the continuum when present at both 1.3 m. and base is nearly the same in oak dominated woods.

Many important species have broad unimodal distributions (Fig. 6C):

Amblystegium varium — *Mnium cuspidatum*
Anomodon minor — *Physcia orbicularis*
Chamberlainia acuminata

P. orbicularis is the only lichen in this group. *Platygyrium repens,* a very common base level species, has little discernible trend in the upland forests, being equally abundant in oak openings, oak woods, and maple woods. *Anomodon attenuatus* and cf. *Lecanora symmicta* occupy a broad range and have rather high frequency in the maple woods where they join *Graphis scripta* (Fig. 6D). The remaining species are of such broad amplitude and low frequency that they are not subject to detailed interpretation.

Comparison of cryptogams at 1.3 m. and base.—Most cryptogams have optimal development at only one level on the trees. Some are important at 1.3 m. and almost completely absent at base, such as *Lecanora subfuscata, Parmelia borreri,* and *Physcia aipolia.* Only three important species at 1.3 m., *Lepraria aeruginosa, Physcia orbicularis,* and *Platygyrium repens,* have even greater importance at base level. Bryophytes and one lichen are especially characteristic of the base level and are virtually unknown at 1.3 m.:

Amblystegium varium — *Cladonia coniocraea*
Anomodon minor — *Entodon* sp.
Chamberlainia acuminata — *Mnium cuspidatum*

The differences between the 1.3 m. and base frequencies are not nearly so pronounced for the other common species. It is interesting to observe, moreover, the gradual shifting of the optimal range of many species up the trunks in the progression from pioneer to climax conditions. *Parmelia caperata* and *P. rudecta,* for example, are more frequent at the base than 1.3 m. level of trees in oak openings, more frequent at 1.3 m. than base in oak woods, and absent at both base and 1.3 m.

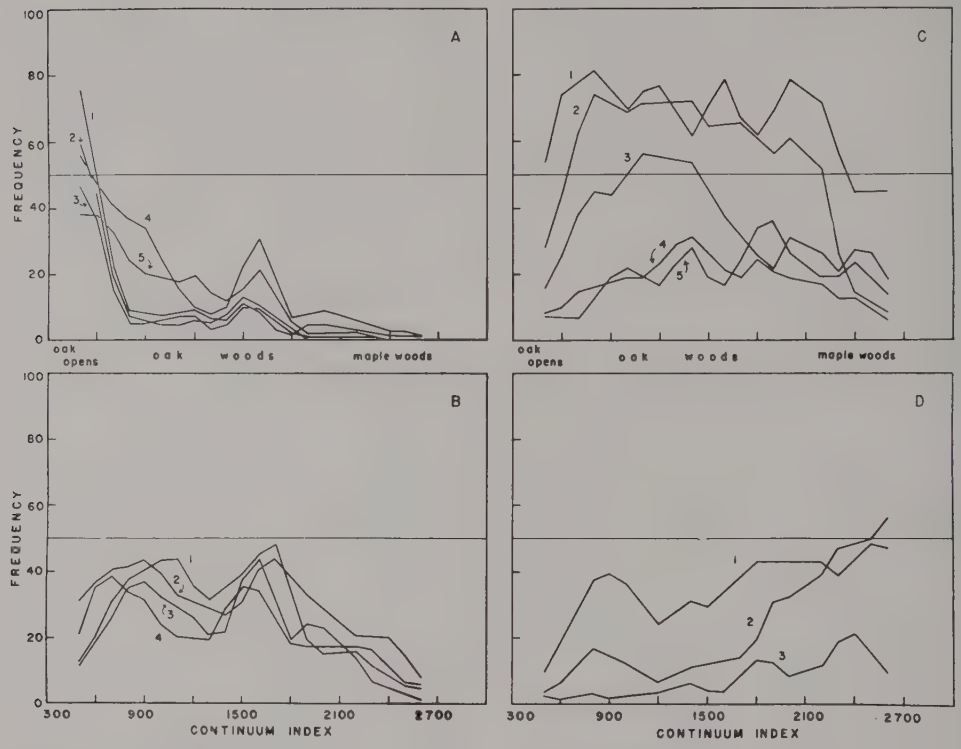

FIG. 6 A-D. Stand frequencies of major cryptogams at base level arranged in order of continuum index. Lines represented as in Fig. 2.

6A: 1, *Physcia millegrana;* 2, *Parmelia caperata;* 3, *Candelaria concolor;* 4, *Parmelia rudecta;* 5, *Cladonia coniocraea.*

6B: 1, *Entodon* sp.; 2, *Allarthonia caesia;* 3, *Parmelia aurulenta;* 4, *Frullania eboracensis; Lepraria aeruginosa,* not graphed, is virtually identical with *Parmelia aurulenta.*

6C: 1, *Physcia orbicularis;* 2, *Mnium cuspidatum;* 3, *Chamberlainia acuminata;* 4, *Amblystegium varium;* 5, *Anomodon minor.*

6D: 1, cf. *Lecanora symmicta;* 2, *Graphis scripta;* 3, *Anomodon attenuatus.*

in maple woods where they were sometimes observed in the canopy. There appeared however to be very scanty development of cryptogamic vegetation in the canopies of trees in the prairie-forest border.

Cryptogamic vegetation of the tree species

Quercus rubra-Q. velutina.—If the floras of *Q. rubra* and *Q. velutina* are carefully compared, great similarities are evident. The frequency of most species (Table III) is similar on either tree in oak woods where 75 per cent of *Q. rubra-Q. velutina* individuals are found. Since the two tree species seem to offer nearly identical substrata for cryptogams, little information can be lost by combining these two tree species for quantitative analyses. There are 45 species of cryptogams of which 17 have frequencies of more than 10 per cent on this tree population (Table IV). The rich vegetation consists of many foliose species, especially Parmeliae, *Physcia millegrana, P. orbicularis,* and crustose *Allarthonia caesia,* often with high coverage (Fig. 7). Among the bryophytes, *Frullania eboracensis* and *Platygyrium repens* are important community members, the latter attaining high coverage. There is an average of about 8.5 species per tree at 1.3 m. The average number varies with the environmental location of the tree, there being only 4 species per *Q. rubra- Q. velutina* in maple woods. Although most species occur with nearly equal frequency in all d.b.h. size classes, some bryophytes, such as *Platygrium repens,* occur on larger trees which have much rougher bark than small trees, while some lichens, for example *Candelaria concolor* and *Physcia aipolia,* unaccountably have maximum frequency on the small trees. However, the average number of species per tree varies insignificantly with

TABLE III. *Frequency of some randomly selected cryptogams at 1.3 m. on individuals of* Quercus rubra *and* Q. velutina *in stands where either tree is the leading dominant*

	Q. velutina	*Q. rubra*
Allarthonia caesia	85	82
Candelaria concolor	44	49
Lecanora subfuscata	38	37
Parmelia borreri	12	26
Parmelia caperata	52	49
Physcia aipolia	31	41
Physcia millegrana	71	66
Platygyrium repens	85	82

TABLE IV. *Frequency of 26 important cryptogams at 1.3 m. on 7 major trees in the upland forests. Only species with 10% frequency on at least one tree are included*

	Quercus rubra-Q. velutina	*Carya ovata*	*Q. macrocarpa*	*Q. alba*	*Ulmus rubra*	*Tilia americana*	*Acer saccharum*
Allarthonia caesia	76	90	28	13	2	27	25
Arthonia radiata	—	8	—	—	1	24	1
Candelaria concolor	47	22	56	22	20	8	2
Frullania ebracensis	64	22	41	13	6	14	5
Graphis scripta	34	61	6	2	—	41	93
Lecanora subfuscata	37	14	—	—	—	—	—
cf. Lecanora symmicta	16	11	2	8	8	20	10
Lepraria aeruginosa	24	9	25	22	6	11	1
Lindbergia austinii	4	1	24	36	24	2	—
Opegrapha pulicaris	1	—	14	23	1	1	1
Orthotrichum pumilum	2	—	22	20	5	1	1
Parmelia aurulenta	69	44	18	10	4	24	5
Parmelia borreri	25	21	31	5	1	1	—
Parmelia caperata	48	13	29	2	—	2	—
Parmelia rudecta	68	38	64	25	5	21	4
Parmelia sulcata	11	7	1	1	—	1	—
Physcia aipolia	42	50	38	13	4	13	2
Physcia elaeina	1	—	7	13	6	3	1
Physcia grisea	7	2	47	55	14	6	2
Physcia millegrana	65	38	62	17	11	22	2
Physcia orbicularis	54	42	33	73	45	51	25
Physcia tribacoides	8	2	41	48	4	3	1
Platygyrium repens	73	12	15	10	7	19	4
Pylaisia selwynii	1	—	22	11	2	1	—
Rinodina papillata	10	4	8	1	—	2	—
Xanthoria fallax	3	—	32	12	9	3	—

d.b.h. The exclusion of trees below 10 cm. d.b.h. apparently precluded the effects of tree size in reducing the flora. Klement's (1952) study emphasizes the fact that trees below 10 cm. d.b.h. support considerably fewer cryptogams than trees above 10 cm.

Variation in the floristic composition of communities on *Quercus rubra-Q. velutina* can probably be correlated with the environment. When species of more than 25 per cent frequency are plotted as percentage occurrence on the trees, arranged in order of continuum index, they fall into three broad communities. One includes simply

FIG. 7. A community of *Parmelia borreri, P. caperata,* and *P. rudecta* and *Physcia millegrana* at 1.3 m. on *Quercus velutina.*

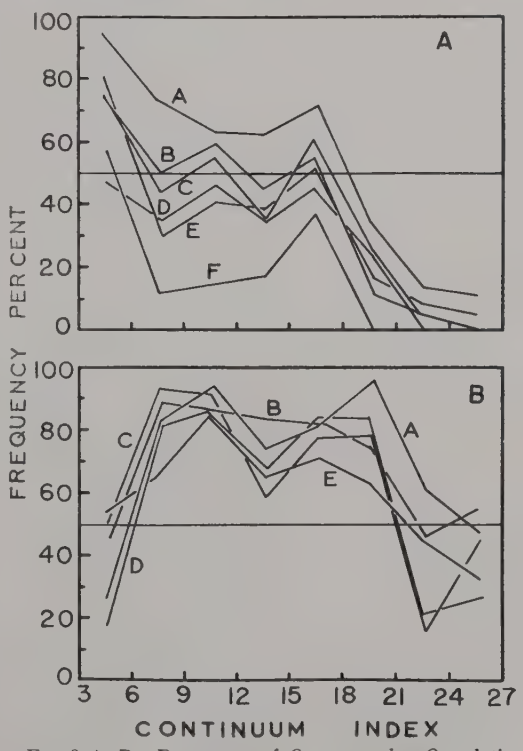

FIG. 8 A, B. Percentage of *Quercus rubra-Q. velutina* individuals by stand arranged in order of continuum index with some important cryptogams at 1.3 m. Lines connect average frequency per 300 unit interval.

8A: A, *Physcia millegrana;* B, *Parmelia caperata;* C, *Candelaria concolor;* D. *Lecanora subfuscata;* E, *Physcia aipolia;* F, *Parmelia borreri.*

8B: A, *Platygyrium repens;* B, *Allarthonia caesia;* C, *Parmelia rudecta;* D, *P. aurulenta;* E. *Frullania ebracensis.*

Graphis scripta which has nearly 100 per cent frequency on *Q. rubra* individuals in maple woods where other cryptogams are very rare, drops rapidly in frequency in oak woods, and is absent from trees in oak openings. Another group (Fig. 8A), *Candelaria concolor, Parmelia borreri* and *P. caperata, Physcia aipolia,* and *P. millegrana,* has a pronounced peak of frequency on *Q. velutina* in oak openings. From 600 to 1800 continuum index they maintain a reduced and irregular level of frequency on *Q. ruba-Q. velutina* and then are not found on trees in basswood and maple stands. A third group (Fig. 8B), has uniformly high frequency on *Q. rubra- Q. velutina* in oak woods with considerably less importance on the trees in both oak openings and maple woods.

At the base level, *Q. ruba-Q. velutina* has 48 species with 17 of them with more than 10 per cent frequency (Table V). Of these, 12 have already been discussed at the 1.3 m. level. Mosses, especially *Entodon* sp., *Mnium cuspidatum,* and *Platygyrium repens,* and the lichen *Cladonia coniocraea* attain high abundance and often high coverage. When plotted along the continuum gradient, they all had maximum frequency on *Q. rubra- Q. velutina* in oak woods. The trees in oak openings had high frequency of *Parmelia caperata* and *P. rudecta* as well as most of the occurrences of certain rarer mosses, especially *Campylium hispidulum, Dicranum montanum,* and *Hypnum reptile.*

As may be deduced from Tables IV and V, *Q. rubra-Q. velutina* has a cryptogamic vegetation noticeably different from the other trees, excepting *Carya ovata.* This difference may be accountable to the bark characteristics. For example, the pH at 1.3 m. is quite low (Fig. 9), the median being 4.9. The bark moisture relations are summarized in Table VI. The hard persistent bark of *Q. rubra* or *Q. velutina* has very low absorptive capacity. Long-lived crustose lichens such as *Buellia stillingiana* and *Pyrenula nitida* and large foliose lichens are frequent on these trees.

Quercus alba.—Eighteen of the 38 species on this common tree have at least 10 per cent frequency at 1.3 m. (Table IV). Only 10 of these have comparable frequency on *Q. rubra-Q. velutina. Quercus alba* has an average of 4.5 species per tree with relatively low coverage.

TABLE V. *Frequency of 22 important cryptogams at the base of 7 major trees in the upland forests. Only species with 10% frequency on at least one tree are included*

	Quercus rubra-Q. velutina	*Carya ovata*	*Q. macrocarpa*	*Q. alba*	*Ulmus rubra*	*Tilia americana*	*Acer saccharum*
Allarthonia caesia	45	75	22	8	3	29	19
Amblystegium varium	5	19	23	38	40	18	4
Anomodon minor	7	13	24	38	33	20	9
Candelaria concolor	13	6	29	3	2	2	—
Chamberlainia acuminata	20	29	29	79	54	28	6
Cladonia coniocraea	39	1	13	1	—	—	1
Entodon sp.	47	17	13	33	11	7	2
Frullania eboracensis	45	41	47	10	7	24	8
Graphis scripta	11	68	1	1	1	38	81
Lepraria aeruginosa	44	26	37	29	7	11	1
cf. Lecanora symmicta	36	57	12	13	23	61	47
Leskea polycarpa	6	13	2	15	27	14	4
Lophocolea heterophylla	11	2	—	1	1	1	1
Mnium cuspidatum	66	38	46	77	37	27	2
Parmelia aurulenta	50	34	12	5	—	18	2
Parmelia caperata	18	11	30	1	—	—	—
Parmelia rudecta	42	19	55	6	—	7	4
Physcia grisea	7	4	38	14	1	—	—
Physcia millegrana	20	6	53	2	1	2	1
Physcia tribacoides	1	1	18	4	7	—	—
Physcia orbicularis	82	80	56	65	34	59	50
Platygyrium repens	80	65	42	13	14	48	66

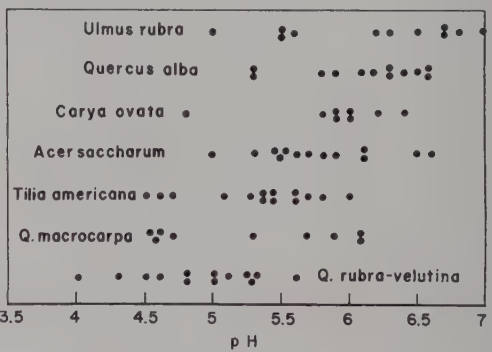

FIG. 9. Individual pH values for bark samples from 7 major trees. Samples of about 1 g. were pulverized, soaked in 6-8 cc. water for 24 hours, and the pH of the solution was measured with a glass electrode Beckmann meter.

TABLE VI. *Values of moisture capacity for 3-10 g. bark samples from 7 major trees (1.3 m. on the south side), expressed as percentage of air dry weight (100%) for given time intervals after saturation with evaporation into a stable atmosphere of 30% relative humidity (22° C.). Values represent averages of 8-10 samples per tree*

	Acer saccharum	*Carya ovata*	*Quercus rubra-Q. velutina*	*Q. macrocarpa*	*Tilia americana*	*Q. alba*	*Ulmus rubra*
Saturated	129	129	133	179	180	194	222
After 1 hr.	120	123	125	162	162	181	206
After 2 hr.	112	117	114	153	146	158	178
After 4 hr.	106	110	105	135	127	128	134
After 24 hr.	102	102	101	101	104	103	102

Physcia is a very important genus along with *Lindbergia austinii* and to a lesser extent *Pylaisia selwynii* and *Orthotrichum pumilum,* all of which are comparatively rare cryptogams on *Q. rubra-Q. velutina.* At the same time, Parmeliae, *Platygyrium repens,* and crustose genera other than pyrenocarpous lichens are quite rare. No crytogams are significantly dependent on size of the tree but occur with similar frequency on all size classes of diameter encountered. The percentage of *Q. alba* individuals with four important species was plotted along the continuum gradient (Fig. 10). All species appear to be members of a community which reaches optimal development in stands dominated by *Q. alba;* trees in the extreme environment of oak openings or maple woods have depauperate remnants of this community or no cryptogams at all.

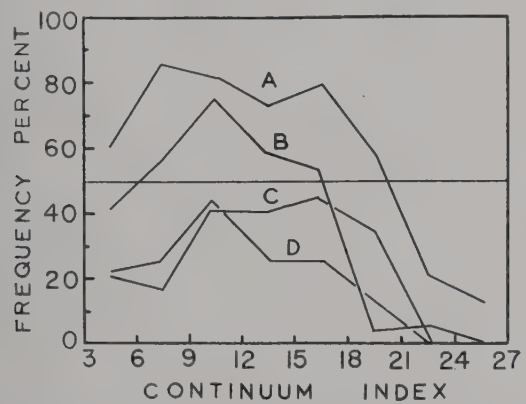

FIG. 10. Percentage of *Quercus alba* individuals by stand arranged in order of continuum index with some important cryptogams at 1.3 m. Lines represented as in Fig. 8. A, *Physcia orbicularis;* B, *P. grisea;* C. *Lindbergia austinii;* D, *P. tribacoides.*

At base level, there were 46 species, 12 of them important and often with high coverage (Fig. 11). The flora is composed chiefly of mosses with only one lichen, *Physcia orbicularis,* attaining dominance. *Amblystegium varium, Anomodon minor, Chamberlainia acuminata,* or *Mnium cuspidatum* very often form dense mats at the base of trees. These species reach optimal development on *Q. alba* individuals where that is dominant. On the other hand, trees in the more climax stands have somewhat higher frequency of *Anomodon attenuatus* (and *A. minor* to a lesser extent) than elsewhere.

The bark characteristics of this tree were studied along with those of *Q. rubra-Q. velutina.* The pH range (Fig. 9) is higher than that of any other tree except *Ulmus rubra,* with a median of

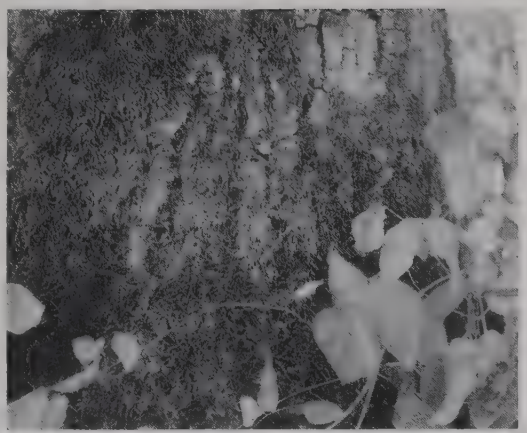

FIG. 11. A community of *Chamberlainia acuminata* (upper half) and *Mnium cuspidatum* at the base of *Quercus alba.*

6.3. *Q. alba* and *Q. rubra- Q. velutina* are even more different with respect to bark moisture capacity (Table VI); *Q. alba* absorbs nearly twice its air dry weight of water. The differences in the physical structure of the bark of the two major trees is also a significant factor. *Quercus alba* has unstable flaky bark which does not permit the establishment of many crustose and foliose lichens.

Acer saccharum.—The vegetation *of A. saccharum* at 1.3 m. is typified solely by *Graphis scripta* (Table IV) which occurs on nearly every individual of this tree. All other cryptogams have far lower frequency so that a maple tree often appears quite devoid of cryptogams. There are only 1.8 species per tree on the average. At base level (Table V), cf. *Lecanora symmicta, Physcia orbicularis,* and *Platygyrium repens* achieve comparative importance along with *G. scripta,* forming a discontinuous mat of vegetation.

The bark characters of *Acer saccharum* do not differ appreciably from those of *Quercus rubra-Q. velutina.* The stand environment created by maple, especially low light intensity, probably transcends host specificity and becomes a limiting factor. In fact, oak trees in maple woods usually have few or no cryptogams, whereas in the absence of a nearby maple, the cryptogams flourish.

Minor trees.—Tilia americana, a frequent component of climax stands, has few important cryptogams (Table IV), with an average of only 3.2 species per tree at 1.3 m. *Arthonia radiata,* a species with very high fidelity for this tree, possesses a high preference for smaller diameter size classes; it was absent from trees larger than 25 cm. d.b.h. which had usually lost the smooth peri-

derm. At base level (Table V), there are a number of species with rather high frequency, especially cf. *Lecanora symmicta, Physcia orbicularis,* and *Platygyrium repens.* In general, however, the cryptogams form only a discontinuous thin mat at both base and 1.3 m. The bark characters are summarized in Figure 9 and Table VI. The pH range is low but moisture capacity is relatively high.

Ulmus rubra is usually a member of climax stands. As Tables IV and V indicate, there are few important species and in fact only an average of 1.9 species per tree. The flora at both 1.3 m. and base levels is similar to that of *Quercus alba* and the bark characters of the two trees are virtually identical.

Carya ovata has 14 important cryptogams, all of which are also important on *Quercus rubra-Q. velutina.* There is an average of 5.4 species per tree, none of them having high coverage. At base level are 16 important species which are also generally important on *Q. rubra-Q. velutina. Carya ovata* resembles the latter tree group with respect to bark moisture capacity (Table VI) but the pH range is higher (Fig. 9).

Quercus macrocarpa is a component of oak openings where it is typically open-grown with little surrounding understory. Of the 9 important species at 1.3 m., some are also of high frequency on *Q. rubra-Q. velutina* individuals in pioneer stands: *Candelaria concolor, Parmelia borreri,* and *Physcia millegrana.* Other species, moreover, are quite as important on *Q. alba*: *Lindbergia austinii, Orthotrichum pumilum, Physcia grisea,* and *P. tribacoides.* Thus, *Q. macrocarpa* has species characteristic of both major trees, *Q. alba* and *Q. rubra-Q. velutina.* There are on the average 7.2 species per tree at 1.3 m., ranking it second to *Q. rubra-Q. velutina* in floristic richness. The vegetation at base follows a similar pattern with relationships to both major trees. The bark of this tree, which is relatively persistent, though not too hard, resembles that of *Q. alba* on the one hand (high moisture capacity), on the other, that of *Q. rubra-Q. velutina* (low pH). (See Table VI and Fig. 9.)

Data on additional minor trees will not be summarized in detail. It appears that *Acer rubrum, Carya cordiformis, Juglans cinerea, Populus* sp., and *Prunus serotina* approach *Q. rubra-Q. velutina* in their bark characteristics and cryptogamic vegetation. *Fagus granifolia* is very similar to *Acer saccharum,* and *Fraxinus americana, Juglans nigra, Ostrya virginiana,* and *Ulmus americana,* all trees with soft bark, resemble *Q. alba* and *U. rubra* very closely.

Statistical association between trees and cryptogams

The above analysis and comparison of the frequencies of crytogams on the various tree species represents a good empirical approach which many workers (*cf.* Waldheim 1944) have found useful. It is possible, however, to study the relationships between the trees by means of a quantitative index of association which places data from all trees on an equal basis. A statistical approach to host specificity has not been explored by earlier workers, and the present attempt will illustrate further the applicability of such analyses to cryptogamic data.

In analyzing association of trees and cryptogams, one would set up a basic assumption or null hypothesis that cryptogams are propagated at random and independent of differences between tree species. In other words, there would be no association between tree and cryptogam. When a tree has far greater frequency of a cryptogam than we would infer on the basis of probability, this tree must either offer an exceptionally favorable substratum for the cryptogam, or the species may seem more frequent on this tree because it is avoiding, so to speak, the individuals of another tree species. If the tree has far less occurrences of a cryptogam than we would predict, we may assume that this substratum is not suitable for growth of cryptogams or that the environment created by the tree prevents growth of them. In either case, the null hypothesis would be rejected.

Let us consider a specific example. *Physcia orbicularis* was found on 96 individuals of *Tilia americana.* Since *P. orbicularis* has a frequency of 51% on trees (1.3 m.) in the upland forests, we would expect to find 96 (.51 x 189 trees) individuals of *T. americana* with the lichen. Since the observed and expected values of joint occurrence agree, the null hypothesis cannot be rejected, for there is no evidence of association between *P. orbicularis* and *T. americana.* This simple calculation can be performed for all cryptogams on the 7 major trees by referring to the data in Tables I, II, IV, and V, where, as a matter of fact, one will discover that most of the species are associated with one or more trees. It would therefore be desirable to measure the degree of tree-cryptogam association by means of Cole's index of interspecific association (Cole 1949) which seems ideally suited for this computation.

The basic information required for the index includes total number of occurrences of a cryptogam and a tree and the number of times the cryptogam was found on the tree in question. These

data are assembled into appropriate formulae as presented by Cole (1949). The resulting values of the index vary from + 100 to − 100 per cent, representing the actual percentage of possible perfect association or disassociation. In the above example, Cole's index equals zero when there is no statistical association between *P. orbicularis* and *T. americana.* If the lichen were found instead on every individual of *T. americana,* there would be 100% association; if on no trees, there would be 100% disassociation.

Tree-cryptogam association at 1.3 m.—Cole's index was computed for the 26 species in Table IV and a number of rarer ones on the 7 principal trees. The results for the important species are presented in Table VII. Some of the positive values are quite high, as for example *Lecanora subfuscata* which attains 92 per cent possible perfect association with *Quercus rubra-Q. velutina;* in other words, the cryptogam was found almost exclusively on this tree group. There are many values of − 100% indicating that the cryptogam was not found on the trees of a particular species at all. The following important cryptogams have high positive association with *Q. rubra-Q. velutina*:

Allarthonia caesia
Candelaria concolor
Frullania eboracensis
Lecanora subfuscata
Parmelia aurulenta
P. borreri
P. caperata
P. rudecta
Physcia aipolia
P. millegrana
Platygyrium repens

This list is the same as the one involving cryptogams which are the major components of the vegetation of the *Q. rubra-Q. velutina* group and which also have similar distributions along the continuum gradient. Some rarer species with high fidelity for this tree group include *Parmelia sulcata, Pyxine sorediata,* and *Rinodina papillata.* The only other tree with a similar alignment of species is *Carya ovata.* The other trees behave quite differently.

Quercus alba has the following species with high positive association:

Lindbergia austinii
Opegrapha pulicaris
Orthotrichum pumilum
Physcia elaeina
P. grisea
P. orbicularis
P. tribacoides
Pylaisia selwynii
Xanthoria fallax

All of these species have unimodal distributions along the continuum gradient, as does *Q. alba,* and form the typical epiphytic vegetation of this tree. They are more or less highly disassociated with *Q. rubra-Q. velutina.* It will be noted that the cryptogamic vegetation of *Ulmus rubra* bears closest resemblance to that of *Q. alba.*

TABLE VII. *Cole's indices of association between 21 important cryptogams at 1.3 m. and 7 major trees, expressed as percentages*

	Quercus rubra-Q. velutina	*Carya ovata*	*Q. macrocarpa*	*Q. alba*	*Ulmus rubra*	*Tilia americana*	*Acer saccharum*
Lecanora subfuscata	92	2	−100	−100	−100	−100	−100
Parmelia caperata	78	− 23	15	− 88	−100	− 90	−100
Platygyrium repens	64	− 58	− 46	− 64	− 77	− 35	− 85
Allarthonia caesia	61	83	− 29	− 66	− 95	− 31	− 36
Parmelia aurulenta	55	21	− 40	− 66	− 85	− 19	− 85
Frullania eboracensis	55	− 19	19	− 52	− 79	− 48	− 83
Parmelia borreri	54	11	22	− 53	− 95	− 90	−100
Parmelia rudecta	53	7	47	− 26	− 85	− 39	− 87
Physcia millegrana	49	10	45	− 48	− 65	− 31	− 95
Physcia aipolia	39	36	20	− 39	− 83	− 39	− 91
Candelaria concolor	34	0	41	− 13	− 23	− 69	− 94
Lepraria aeruginosa	25	− 43	11	14	− 61	− 24	− 98
Physcia orbicularis	7	− 18	− 35	46	− 12	1	− 51
Physcia tribacoides	− 31	− 79	34	44	− 68	− 72	− 91
Xanthoria fallax	− 52	−100	28	33	3	− 54	−100
Physcia grisea	− 63	− 87	35	57	− 26	− 67	− 92
Orthotrichum pumilum	− 67	−100	17	53	− 26	− 92	− 96
Lindbergia austinii	− 72	− 94	13	56	13	− 87	−100
Physcia elaeina	− 86	−100	25	60	2	− 38	− 94
Opegrapha pulicaris	− 88	−100	9	82	− 88	− 90	− 96
Pylaisia selwynii	− 97	−100	19	60	− 62	− 86	−100
Arthonia radiata	−100	10	−100	−100	− 90	62	− 79
Graphis scripta	4	43	− 81	− 92	−100	14	89

Quercus macrocarpa overlaps in behavior both *Q. alba* and *Q. rubra-Q. velutina.* About half of its positively associated species are common on the former tree, the other half on the latter tree group. *Tilia americana* and *Acer saccharum* have so many negative values that they cannot be compared easily with the other trees. The high positive values for *Arthonia radiata* and *Graphis scripta* typify the flora of these trees respectively. In addition, *Rinodina halei* occurred almost exclusively on *A. saccharum.*

Tree-cryptogam association at base.—Cole's index values were computed for 27 species which are important at the base level. Fourteen of these were treated in the analysis at 1.3 m., and their behavior at base is not significantly different from that at 1.3 m. The remaining species are confined principally to the base level.

Quercus rubra-Q. velutina has a number of important crytogams with high positive association:

Cladonia coniocraea
Entodon sp.
Lophocolea heterophylla
Lepraria aeruginosa
Mnium cuspidatum
Physcia orbicularis
Platygyrium repens

Most of these are disassociated with *Q. alba.* Some rare species, *Anaptychia speciosa, Brachythecium* sp., and *Dicranum montanum,* also have high fidelity for this tree group.

The second leading tree, *Q. alba,* has several positively associated species:

Amblystegium varium *Chamberlainia acuminata*
Anomodon minor *Mnium cuspidatum*

All of these bryophytes, with the notable exception of *M. cuspidatum,* appear to avoid individuals of *Q. rubra-Q. velutina.*

Cryptogams are distributed at the base of the minor trees in general as at 1.3 m. *Ulmus rubra* resembles *Q. alba, Carya ovata* resembles *Q. rubra-Q. velutina,* while *Q. macrocarpa* has similarities with both major trees. Certain species with maximum importance at the base level have much higher values of association here than at 1.3 m. of the same tree species, as the case of *Platygyrium repens* on *Acer saccharum.* This fact emphasizes the relative nature of the index.

Sociological relationships of the cryptogams and tree species.—An examination of the Cole's index values for species at base or 1.3 m. reveals the following gradient of tree species:

Q. rubra-velutina → *Carya ovata* → *Q. macrocarpa* → *Q. alba.* Within the gradient there is a progressive decrease in the index values for Parmeliaceae and an increase for the Physciaceae toward the right. The cryptogamic vegetation of *Q. rubra-Q. velutina* and *Q. alba* are quite dissimilar while the other trees occupy an intermediate position.

This order of tree species, erected on an objective analysis of the Cole's index values, appears to correlate with the bark characters of each tree previously discussed. For example, the data in Table VI show an excellent correlation with increasing moisture capacity, which also reflects a physical gradient from hard persistent to porous flaky bark. The pH data provide a less satisfactory basis, yet this factor has an importance in the early growth stages of cryptogams (*cf.* Ikenberry 1936), especially when one deals with *Q. alba* (median pH 6.3) and *Q. rubra- Q. velutina* (median 4.9). It must be admitted that correlation of the cryptogamic vegetation with bark factors is largely speculative in the absence of more extensive physiological studies on growth and nutrition of cryptogams. The widespread attempts to find a basis for correlation are certainly shortsighted until one proves with suitable quantitative data that the cryptogamic vegetation of the various trees is actually different.

INTERSPECIFIC ASSOCIATION OF CRYPTOGAMS

The use of various techniques, such as continuum plotting and analysis of individual tree data, has demonstrated that many cryptogams have similar ecological requirements. It would be profitable to investigate formally the interrelations of the cryptogams themselves independent of the host or environment and to measure the biological similarity of the species. Such a study will offer more than a purely statistical manipulation, for the data from interspecific association may be applied to an interpretation of community structure.

Cole's index analysis

The first analysis is concerned with the joint occurrences of species in pairs on the 2797 trees. Consider two species each having a frequency of 20 per cent on the trees. Proceeding on the assumption that the two species are distributed at random and independently, we can predict the probability of finding them together on the same

TABLE VIII. *Matrix of Cole's indices of association between 21 important cryptogams at 1.3 m., expressed as percentages. Values which are statistically insignificant at the 5% level with chi-square are in italics*

	L. s.	*P. a.*	*A. c.*	*P. r.*	*F. e.*	*P. r.*	*P. c.*	*P. m.*	*P. b.*	*C. c.*	*P. a.*	*L. a.*	*G. s.*	*L. s.*	*P. o.*	*O. p.*	*P. t.*	*X. f.*	*L. a.*	*P. s.*	*P. g.*
Lecanora subfuscata	.....	73	67	66	66	73	61	57	27	46	31	20	*0*	7	17	−52	*2*	−63	−65	−100	−58
Parmelia aurulenta	.....	.....	60	57	52	61	61	39	35	30	22	46	7	39	29	−55	*6*	*− 7*	−31	*−18*	*−10*
Allarthonia caesia	.....	.....	.....	56	42	43	53	37	35	19	38	22	18	26	5	−72	−29	−40	−59	−67	−49
Platygyrium repens	.....	.....	.....	.....	60	54	50	38	30	22	15	40	*3*	35	24	−43	*0*	−31	−32	−61	−25
Frullania eboracensis	.....	.....	.....	.....	.....	55	57	40	42	31	17	37	*0*	30	27	9	14	*3*	*0*	13	*4*
Parmelia rudecta	.....	.....	.....	.....	.....	.....	71	45	46	37	31	43	−12	29	15	*−15*	30	19	*− 1*	*9*	11
Parmelia caperata	.....	.....	.....	.....	.....	.....	.....	67	56	53	40	14	−35	*−11*	*2*	*−27*	6	*5*	−48	−45	−28
Physcia millegrana	.....	.....	.....	.....	.....	.....	.....	.....	68	36	49	9	−30	8	*− 1*	*− 8*	−26	*−20*	−40	−62	−33
Parmelia borreri	.....	.....	.....	.....	.....	.....	.....	.....	.....	55	54	*− 9*	−44	−46	*4*	*2*	6	8	*−21*	*−41*	*− 4*
Candelaria concolor	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	35	17	−47	*−10*	29	16	34	30	11	14	19
Physcia aipolia	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	−35	−40	−35	*6*	*− 2*	*− 7*	10	−42	−57	−21
Lepraria aeruginosa	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	−16	21	45	13	26	15	17	40	22
Graphis scripta	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	20	−11	−87	−64	−86	−91	−97	−81
cf. Lecanora symmicta	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	54	*− 1*	*2*	*1*	*3*	*1*	*4*
Physcia orbicularis	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	67	46	49	49	40	54
Orthotrichum pumilum	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	24	16	36	27	58
Physcia tribacoides	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	41	30	40	67
Xanthoria fallax	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	46	26	68
Lindbergia austinii	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	59	56
Pylaisia selwynii	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	79
Physcia grisea	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

tree as .2 x .2, the product of their frequencies, that is 4 per cent of the trees should have both species. It would be desirable to measure the departure from randomness of the known values of joint occurrence. Cole's index is the most suitable tool for this computation. The index will equal zero if 4 per cent of the trees have both species which then would be distributed independently; + 100 per cent if they always occurred on the same trees; and − 100 per cent if they never occurred together.

Cole's index was used to compute interspecific association between the 42 most frequent cryptogams on the 2797 trees. After these values were obtained, the signficance of each was tested with chi-square. The t test is equally suitable since t^2 was found to approximate chi-square with an error of about ± 1 per cent throughout the range of values. The standard error was also computed but not used other than to calculate t. The final results for 21 important species at 1.3 m. are given in a matrix (Table VIII). The order of the species along the axes was determined empirically. In such a matrix, it is customary to arrange the highest values along the diagonal (*cf.* Agrell 1945) such that groups of species with high mutual association will become more apparent visually. Some of the values are unexpectedly high when positive, indicating that many of the species occur together more often than would be predicted. For example 60 per cent possible perfect association is realized between *Allarthonia caesia* and *Parmelia aurulenta,* two common species in the upland hardwoods. Many species, however, are not significantly associated or have high negative association. In the matrix large groups of species have consistently high values of association with one another. One obvious group includes

Allarthonia caesia
Candelaria concolor
Lecanora subfuscata
Frullania eboracensis
Parmelia aurulenta
P. borreri
P. caperata
P. rudecta
Physcia aipolia
P. millegrana
Platygyrium repens.

These species, it will be recalled, have in common a high degree of host specificity for *Quercus rubra-Q. velutina* and at the same time occur with lower than expected frequency on *Q. alba* and related trees. Another distinct grouping has these members with high mutual association:

Lindbergia austinii
Orthotrichum pumilum
Physcia grisea
P. orbicularis
P. tribacoides
Pylaisia selwynii
Xanthoria fallax

As a group, they prefer *Q. alba* as a host and with the exception of *P. orbicularis* have very low frequency on *Q. rubra-Q. velutina.* The members of each of the above two groups are generally negatively or insignificantly associated with those of the other group. Still another group of species, *Graphis scripta,* cf. *Lecanora symmicta,* and *Lepraria aeruginosa,* show little positive association with either of the major groups. It is known that they have little or no preference for *Q. alba* or *Q. rubra-Q. velutina.*

The values in the matrix, then, fall generally into a gradient which reflects primarily the differences in host specificity between the cryptogams. Hence a Cole's index analysis where all trees are treated together is highly dependent on the magnitude of host specificity for cryptogams in the upland forests. It has, in fact, offered an independent means of recognizing the effect of this important factor. Species with high specificity for the same tree have high positive association when taken in pairs; species with little marked specificity are not usually significantly associated with other species. Because of this factor, cryptogams with similar ecological amplitude along a gradient, such as *Parmelia aurulenta* and *Physcia grisea,* have significant disassociation because they are usually found on different tree species.

It is conceivable that two species with high preference for one tree may be distributed at random on that tree, although a Cole's index value for their occurrence on all trees may indicate high positive association. It is necessary, therefore, to determine the association of cryptogams on the same tree species so as to remove the variable of host specificity. This analysis must here be confined to *Q. rubra-Q. velutina* not only because this tree group has more important cryptogams than any other in the region but because a large sample of trees is available. It seemed expedient to include only species of moderately high frequency on and definite specificity for *Q. rubra-Q. velutina.* In one analysis, all 818 *Q. rubra-Q. velutina* individuals were studied. Eleven major species, taken in pairs, were analyzed with Cole's index (see Hale 1953). Data on these cryptogams can be obtained by reviewing Table IV and Figure 8. There appear to be two relatively distinct groups of species. One includes

Candelaria concolor
Parmelia borreri
P. caperata
Physcia aipolia
P. millegrana

which have high positive association with each other. These species reach optimal development on *Q. velutina* in oak openings as a glance at Figure 8A will show, and they lose importance

on *Q. rubra* individuals in the interval 2200 index where *Tilia americana* assumes a dominant role. None of them reach very high frequency in oak woods. The other highly associated group includes

Allarthonia caesia	*Parmelia aurulenta*
Frullania eboracensis	*P. rudecta*
Lecanora subfuscata	*Platygyrium repens*

all of which have very similar curves of frequency on *Q. rubra* and *Q. velutina* (Fig. 8B). In addition, they have maximum frequency in the oak woods and minimum in oak openings and in maple woods. This Cole's index analysis measures the relative effect of environment on cryptogamic distribution, and the species can be grouped according to their index values into communities which have already been recognized by different techniques.

A second analysis was instigated to study interspecific association of cryptogams on *Q. rubra-Q. velutina* individuals in a relatively uniform environment, thereby eliminating this variable which was operative in the former analysis. The same 11 species treated above were tested with Cole's index in the range of oak woods, where there were 647 individuals of the two trees. Of the 55 values, only 2 were statistically insignificant; the remaining values were uniformly high (30-75%) and all positive, with the result that no groups could be segregated from the matrix. Many cryptogams are still highly associated even on the same tree species in a relatively uniform environment.

Community structure

Although some groups of cryptogams appear to behave in remarkably similar fashion toward two variables, host specificity and stand environment, the organization of these species has not been stressed. It might be desirable however to investigate certain statistical aspects of the basic community structure. A Cole's index analysis is somewhat restricted in scope since it proceeds on data in contingency tables where only two species can be considered at a time. Phytosociologists prefer to study as an integrated unit the full complement of species which comprise a community. Such a course calls for data on joint occurrences of 3 or more species on the individual trees. The extraction and statistical analysis of such data are fraught with difficulties not easily appreciated, a more formidable one hinging on the lack of a suitable test of association comparable to Cole's index. Hence the following discussions will be founded on observed numerical values of joint occurrence.

The analysis of many possible mathematical combinations of 3, 4, 5, . . . 11 species on the same individuals of *Quercus rubra-Q. velutina* was undertaken systematically with the same 11 species tested with Cole's index. Any recognizable aggregation of cryptogams which nominally inhabit this tree would logically have high host specificity for and high frequency on it. All 11 for example were found on 20 of the 818 trees at 1.3 m. Reduction to combinations of 10, 9, . . . 5 species produced a very large mass of data in which definite patterns were traceable. Four species, *Candelaria concolor, Parmelia borreri, Physcia aipolia* and *P. millegrana,* formed a group which had greater affinity with each other than with the remaining species. It was discovered for instance that 50 per cent of the *Q. rubra-Q. velutina* in oak openings have this combination of species, whereas only 12 per cent of the same tree species in the oak woods had it. This basic group then appears to form a recognizable community in the oak openings.

The remaining 7 species had greater affinity with each other than with the above 4. No matter what combinations were taken, members of the most frequently occurring groups included 3 or more of the following:

Allarthonia caesia	*P. rudecta*
Frullania eboracensis	*Platygyrium repens*
Parmelia aurulenta	

All five of these occurred on 35 per cent of all *Q. rubra-Q. velutina.* By obtaining the product of their frequencies, it was calculated that this combination occurred on more than twice as many trees as would be expected. Furthermore, in 99.5 per cent of the cases the combination was found on oak trees in the oak woods (600-1800 continuum index), where about 75 per cent of the tree individuals are located. Any combination of 4 of the 5 species recurred on about 40 per cent of the trees, any combination of 3 on 50 per cent. The two rarer species, *Lecanora subfuscata* and *Parmelia caperata,* could be combined with either the oak openings or the oak woods groups; in any event the frequency of the resulting combination dropped. In the second group of 5, addition of either species reduced the observed frequency to 20 per cent.

The nature of the communities on *Quercus rubra* and *Q. velutina* may best be comprehended by regarding them as mathematical combinations of two or more species which occur together more frequently than we would predict from probability. If the species were all distributed at random, it is doubtful if different communities could

be distinguished at all. The above association analysis however proves that the cryptogams are highly associated and fall into definite groupings which reach maximum frequency only in certain forest types. If one should desire to erect a formal nomenclature for the associations on *Q. rubra-Q. velutina,* it would be necessary to decide beforehand which species would characterize each association, how frequent they should be, and how often they should occur together. This procedure is limited only by the total mathematical combinations of the existing flora.

Conclusions

This study has attempted to show the relation of the cryptogamic vegetation to forest types and to tree species and the interrelations of the cryptogams themselves. The emphasis on methodology has produced results of definite statistical reliability, the author believes, because of the large sample sizes employed, and has made possible the statistical analysis of the factors limiting the distribution of cryptogams. The advantages of this approach over purely descriptive methods are fairly obvious and warrant serious consideration if the phytosociology of cryptogams is to progress substantially.

In the upland forests, stand composition is of utmost importance in limiting the distribution of cryptogams. All forest types from pioneer to climax were sampled objectively regardless of the cryptogamic vegetation existing in them. When the stand frequencies of the cryptogams were plotted along the continuum index gradient, each species attained maximum frequency in definite portions of that gradient. They could be classified into several groups, each having similar distribution. One group had maximum frequency in the pioneer oak openings and another peaked in oak woods. Indeed, the majority of cryptogams were most frequent in stands dominated by *Quercus* and usually rare or absent in more mesic stands. A very few species had maximum abundance in climax maple stands. With our present knowledge of the upland forests, we do not expect to find large foliose lichens in maple woods or *Graphis scripta* in oak openings. Variations in the cryptogamic vegetation on each tree species can also be correlated with stand environment. Light intensity appears to be a significant environmental factor in the upland hardwoods with pioneer oak openings received more than 10 times as much light as climax maple woods.

This problem has been given some attention by other workers. Wiśniewski (1929) for instance concluded that in Poland there was little relation between cryptogamic and forest associations. Hilitzer (1925) in a very comprehensive study reached the same conclusion with the qualification that some differences may be accentuated by sampling associations in forests of widely different composition. In the United States, Phillips (1951) decided that bryophytic associations are not always correlated with tree climaxes. Less extensive but careful studies by Patterson (1940), however, indicate that the cryptogamic vegetation is measurably influenced by environment, especially evaporational tension and light intensity. The majority of cryptogamists to be sure have not been directly concerned with this broad subject. The author's data stand in apparent disagreement with a number of previous results. This may be explained in part by the fact that few workers examine objectively the full range of stands in a single floristic province whether they contain cryptogams or not, but rather concentrate on stands with conspicuous epiphytic communities. Determination of stand environment and its effect on cryptogamic vegetation should rest on an objective analysis of an adequate sample of the forest types in a region.

Although the influence of forest environment has not received rightful attention, host specificity and its effect on distribution of cryptogams are comparatively well-known. Hilitzer (1925) has made this point succinctly: "c'est la spécificité de l'arbre." Billings and Drew (1938), Martin (1938), and Wiśniewski (1929) among others implicitly state the importance of tree species in its effect on the floristic makeup of a cryptogamic community. Phillips (1951) reached the surprising conclusion that tree species is not very important. In spite of the convictions of these and other workers regarding host specificity, their conclusions are not always based on adequate data. Many if not all cryptogamists examine only trees bearing cryptogams. This qualification alone poses a serious objection to their conclusions since the degree of host specificity can be controlled by selecting only those trees having a particular cryptogam and ignoring other trees.

In the upland forests, the author had available a very large sample of the tree species selected without regard to what cryptogams were on them. Quantitative analysis of tree-cryptogam association showed that nearly every cryptogam in the flora has preference for a certain tree or tree group and avoids other trees. *Quercus rubra-Q. velutina* and *Q. alba,* the two most numerous trees, each have very different cryptogamic flora and the minor trees are intermediate between them. Each tree has its own peculiar combination of species.

Host specificity has maximum effect on the cryptogamic vegetation in stands from a relatively narrow environmental range. The probability of finding a species in a particular stand is dependent on the relative proportions of the tree components there, and in very small intervals, stand to stand variation of the cryptogamic vegetation can be correlated in large part with variations in tree composition. Host specificity is quite relative, for the same species can have different degrees of association at base and 1.3 m. of the same tree. Host specificity could be correlated to some extent with bark pH and moisture capacity. The correlation was valid only in small segments of the continuum gradient since the environment of widely separated stands appeared to supercede bark as a limiting factor. For example, a *Quercus* individual in a maple woods will have species typical of the climax environment and not of the more xeric oak woods. The interaction of host specificity and environment account for much of the variation in the crytogamic vegetation.

Interspecific association was studied independently of the above factors. Association analysis with Cole's index appears to have possible application as an independent tool in vegetational study in addition to providing a statistical measure of biological similarity. Through simple analysis of joint occurrences it offers an entirely objective means of recognizing the effect of various ecological factors, information which can of course be derived or substantiated by less objective methods. In this study, an analysis carried out independently of tree species differences clearly brought out groups of species, each of which had previously been shown to possess definite requirements of host specificity. When one tree group, *Quercus rubra-Q. velutina,* was analyzed in order to remove this variable, most cryptogams were still highly associated within two groups, one group of species most frequent in oak openings, the other in oak woods. At this level, the environmental requirements of the various cryptogams predominated. Even in the relatively uniform environment of the oak woods, species on *Q. rubra-Q. velutina* were significantly associated. The Cole's index values may be interpreted as measuring the degree to which host specificity and gross environment prevent a random distribution of cryptogams in the upland forests. The groups of species with high association emerging in a Cole's index analysis may be regarded as communities which represent combinations of species with similar ecological requirements.

Our knowledge of the frequency distribution and association of cryptogams in the upland forests of southern Wisconsin has been advanced considerably through the use of relatively simple methods. The probability of finding one or more species on a randomly selected tree is a function of the species of tree selected, the relative proportions of other trees in the same stand which contribute to gross environment, and the presence of certain other cryptogams on the same tree. This investigation has endeavored to reduce at least a few of the complex interacting variables affecting the distribution of cryptogams into statistical quantitative terms.

Summary

An investigation of the corticolous cryptogamic vegetation in the upland forests of southern Wisconsin was initiated in 1951. Seventy-two stands of vegetation were located in 25 southern and southwestern counties. The stands, each from 15-300 acres in extent, were sampled with the random pairs methods of forest ecology. Two cylindrical quadrats girdling the trunk at 1.3 m. and base were examined on each of 2797 trees, using a species-presence method. The final data for 1.3 m. were punched on IBM cards to facilitate statistical analysis.

Within the study area, 33 species of bryophytes and 55 species of lichens were collected. The prairie-forest border has a distinctive flora with little relationship to the northern conifer-hardwoods element. The most satisfactory method of organizing stand data was the use of the continuum index. The basic frequency data were analyzed with various statistical techniques in an effort to measure the relative effect of environment and stand composition and host specificity on the distribution of cryptogams. The pioneer oak openings and the climax maple woods have completely dissimilar cryptogamic vegetation. The mesic oak-dominated woods have a vegetation composed of species with low importance in either of the other forest types. At the stand level, the influence of host specificity is of greatest significance. Variations in the cryptogamic vegetation of stands with relatively similar environment were accountable to changes in the relative density of the tree components, principally *Quercus alba* and *Q. rubra-Q. velutina.* Measurments of environmental factors, such as light, bark pH, and bark moisture, appear to correlate with the data from statistical analysis. A study of interspecific association with Cole's index proved useful in measuring the relative effect of host specificity and environment in preventing a random distribution of cryptogams. The aggregation of many cryptogams into more or less ob-

vious communities was best regarded as a statistical association of species with similar ecological requirements.

The cryptogamic vegetation of different stands and tree species in the upland hardwoods is controlled by a number of interacting variables. The basic frequency data afforded an excellent means of establishing quantitative indices of some of these variables.

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THE EFFECT OF FLOODING ON DEVELOPMENT AND SURVIVAL OF THE LARCH SAWFLY *PRISTIPHORA ERICHSONII* (TENTHREDINIDAE)[1]

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Introduction

Several phases of the ecology of the larch sawfly have been investigated since 1940 at the Forest Biology Laboratory, Winnipeg. During these studies it became apparent that ground moisture is an important factor governing larch sawfly development and survival. This can be readily appreciated when it is realized that (a) cocoons of the larch sawfly spend about ten months or more per year in the moss or duff, and (b) in its natural habitat in the Prairie Provinces and adjoining areas in Canada and the United States the insect is usually found in bogs.

Preliminary studies (Lejeune and Filuk 1947) showed that under certain experimental conditions cocoons of the larch sawfly could be killed by flooding. More detailed studies carried out in 1949 and 1950 have helped to explain these water relationships more fully. This paper reports the results of this later work.

Life History of the Larch Sawfly

The general life history and habits of the larch sawfly (*Pristiphora erichsonii* (Hartig)) have been adequately described in other papers (Lejeune 1947; Watson 1931). Therefore only aspects pertinent to this investigation will be mentioned here.

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Sawfly adults emerge during May, June, and July and lay their eggs in the new terminal shoots of tamarack. The larvae that hatch from these eggs feed on the foliage. When fully grown, they drop to the ground, burrow into the moss or duff, and spin tough, brown, parchment-like cocoons in which they pass the winter. The main period of larval drop is during July and August.

The winter is spent as a last-instar larva in diapause in the cocoon. Most larvae resume development in May or June of the following year and transform to pupae and adults within the cocoon. A number of cocooned larvae, sometimes as high as 25 per cent, may remain in prolonged diapause for two or more winters.

The following stages of the larch sawfly occur in cocoons; eonymph, pronymph, pupa and unemerged adult. All except the eonymph are post-diapause stages. The terms eonymph and pronymph were devised by Eliescu (1932), and were employed by Prebble (1941) in his work on the European spruce sawfly. Though Prebble's morphological descriptions do not correspond exactly with those found in the larch sawfly, analogous eonymph and pronymph phases were recognized.

General Methods and Procedures

Field studies were carried out in the Whiteshell Forest Reserve, Manitoba, and some laboratory studies were conducted at Winnipeg. Controlled flooding treatments were carried out in the field with overwintered cocoons and with newly formed cocoons. In May, 1949, cocoons which had overwintered were collected in a tamarack bog in the Whiteshell Forest Reserve near Telford, Manitoba. During July, 1949, new cocoons were collected from the same bog for experimental purposes. In 1950, new cocoons were obtained by allowing full-grown larvae to drop into and spin up in specially constructed traps placed underneath the tree crowns.

A standardized procedure was followed for most water immersion treatments. After being collected, cocoons were layered in moss in 8-by-12-inch rectangular wooden-framed cages 6 inches deep. The tops and bottoms of the cages were covered with 16-mesh-to-the-inch wire screen. For treatment, cages containing cocoons were submerged in water in pits in a tamarack bog. When not submerged, the cages were placed in a well drained location in moss in the same tamarack bog. Nearly all checks and treatments were replicated once.

The effect of flooding was determined by removing samples of 20 cocoons from each cage prior to immersion and at regular specified intervals following flooding. The cocoons were opened and the condition and stage of development of the insects recorded. For dead insects the cause of mortality was recorded wherever possible, *i.e.* death due to flooding, disease, parasites, predators, etc. The following developmental stages were also noted; eonymph, pronymph, pupae (sometimes subdivided into early and late pupae) and unemerged adults.

In the analysis of the data, the total mortality of treated insects, which included factors such as parasitism and disease, was compared with the total mortality of untreated material.

Special experiments were carried out, as needed, to confirm results obtained from the standardized mass treatments described above. The methods for these are described in their appropriate sections.

Normal Development in Cocoons

To interpret properly many of the effects of ground moisture, it was necessary to determine the normal pattern of post-diapause development in cocoons. The percentage of post-diapause stages present was determined in the spring of 1949 for unflooded caged cocoons examined at two-week intervals, and for cocoons collected in a well-drained location in the field at weekly intervals. One hundred and twenty cocoons were examined each time for the caged material, and 100-200 cocoons for each field collection. The data are summarized in Figure 1.

The maximum numbers of post-diapause stages within cocoons in 1949 were found roughly during the period June 8 to June 25. After most of the sawfly adults emerged, the sawflies remaining in cocoons were mainly eonymphs in prolonged dia-

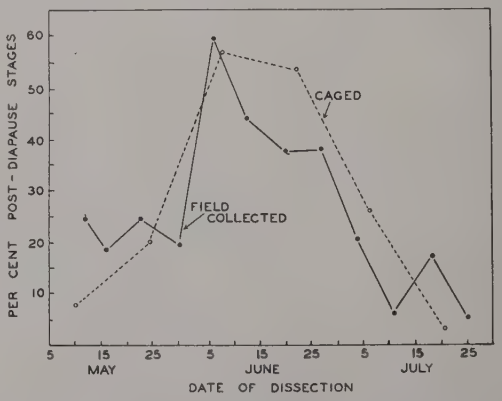

Fig. 1. Occurrence of post-diapause stages in unflooded caged cocoons and field-collected cocoons in 1949.

pause. There was no significant difference between the trends shown by experimental and field material.

Similar checks on normal development in 1950 showed the same trend, but the events occurred about one week later than in 1949. Maximum occurrence of post-diapause stages was from June 15 to June 30.

Effects of Flooding

Larvae in Diapause

On May 10, 1949, two cages containing cocoons were submerged in the experimental tamarack bog mentioned under Methods. All larvae were in the eonymph phase when flooding started. A sample of 20 cocoons was removed from each cage every two weeks and examined to determine mortality.

The experiment was repeated in 1950 with slight modifications. Two cages containing larch sawfly cocoons were submerged on May 23. After two weeks, 20 cocoons were removed from each cage at two-day intervals and dissected. The results of these experiments are shown in Figure 2. In each year data from two replications were pooled.

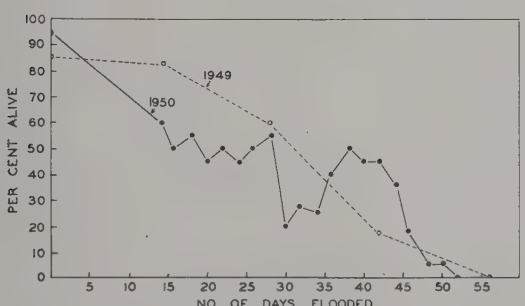

Fig. 2. Survival of larch sawfly larvae in diapause when submerged in water in 1949 and 1950.

In 1949, after 56 days of flooding, all the larvae were dead. In 1950, with more frequent dissections, all larvae were recorded as dead after 52 days. In neither 1949 nor 1950 were there significant differences between replications. From these experiments it can be concluded that about 50 days of continuous flooding during the spring months are required to cause complete mortality of overwintered eonymphs. Flooding for shorter periods, however, can produce heavy mortality. Though larvae in diapause are highly resistant to immersion and well adapted to their habitat, it is evident that flooding in the spring, if sufficiently prolonged, can kill a considerable proportion of insects in diapause.

Post-Diapause Stages

Analysis of data collected in 1949 indicated that post-diapause stages of the sawfly in cocoons succumbed much more readily to flooding than eonymphs. Post-diapause stages referred to are the pronymph, pupa, and unemerged adult.

In 1950, an experiment was conducted to determine the period of flooding necessary to kill 100 per cent of the post-diapause stages. Cocoons were collected from one tamarack bog in the autumn of 1949 and stored through the winter in cages in the bog. In the spring of 1950, cocoons were placed in the standard treatment cages, 400 per cage. Two cages were submerged on June 15, and two on June 24. These dates were selected to ensure the presence of a maximum number of post-diapause stages in the treated material. Twenty cocoons were removed for examination from each cage daily after treatment was started. Data from all cages were pooled and summarized in Table I. Insects that died from parasitism, disease or other causes not attributable to treatment were omitted from the analysis. There was no evidence that any further development took place in the cocoons while they were under water.

Table I. *Mortality of eonymphs and post-diapause stages of the larch sawfly as related to period of flooding*

Days flooded	Eonymphs		Pronymphs		Pupae	
	Cocoons dissected	% dead	Cocoons dissected	% dead	Cocoons dissected	% dead
1-2	46	1.0	30	0.0	24	16.7
3-4	35	0.0	44	50.0	34	61.8
5-6	49	2.0	28	53.6	25	96.0
7-8	53	17.0	31	71.0	20	100.0
9-10	50	22.0	25	84.0	22	100.0
11-12	41	29.3	35	85.7	18	100.0
13-14	39	28.2	36	86.1	25	100.0
15-16	58	50.0	22	81.8	21	100.0
17-18	48	56.2	17	82.4	23	100.0
19-20	37	45.9	11	90.9	20	100.0
21-22	24	58.3	13	100.0	16	100.0

Table I shows that 22 days after flooding, about 50 per cent of the eonymphs were still alive. In contrast, 50 per cent of the pronymphs were dead after three to four days of flooding, and over 50 per cent of the pupae were killed by that time. All pronymphs were dead after 22 days of treatment and all pupae were dead after six days of flooding.

It is interesting to observe that in Table I the mortality of eonymphs and pronymphs appears to increase by "steps," and that at each "step" the percentage of dead insects remains at about the same level for some time. This suggests that there may be physiological sub-phases within the

eonymph and pronymph phases which exhibit different tolerance responses to flooding.

A similar experiment was carried out on a series of cocoons in which the stage of development of the insect in the cocoon before treatment was determined by means of an insect respirometer (Smith and Douglas 1949). The stage was determined on the basis of rate of oxygen consumption. Only insects in post-diapause stages were used. The results paralleled those shown in Table I. A few pronymphs were still alive after 21 days of immersion, but mortality was approaching 100 per cent. All pupae were killed in five days and all unemerged adults were dead after two days.

From data presented, it is clear that pronymphs and pupae are much more susceptible to flooding than eonymphs. The closer the insect is to the adult stage, the more quickly does it succumb to flooding.

Seasonal Flooding

The results obtained in the preceding sections suggested that there is a critical period during spring and early summer when field populations of cocoons are highly susceptible to flooding. From the data it was postulated that this critical period is associated with the maximum occurrence of post-diapause stages in cocoons.

To test this hypothesis the percentages of adults that emerged from cocoons flooded for various periods at different times of the season were determined. Cages containing 180 cocoons each were submerged on May 11 and 25, June 8 and 23, and July 8 and 21, 1949. On each date the following cages were flooded: two for one week, two for two weeks, and two for four weeks. Emergence data are shown in Figure 3B. The histograms for May 11 to June 8 inclusive represent adults that emerged following treatment, since none emerged prior to flooding. The histograms from June 23 on include adults that emerged both before and after the flooding treatments. It was not considered necessary to separate these as the main problem was to determine the overall effects of flooding on survival. For comparative purposes Figure 3A shows the incidence of post-diapause stages in untreated caged cocoons during 1949 on the same time scale. As samples of 20 cocoons were removed from the flooded cages every two weeks to determine the condition of the insects, allowances for cocoons removed had to be made in computing the percentage of emergence of adults.

There is an inverse relationship between the maximum occurrence of post-diapause stages and the percentage of adult emergence. Cages flooded

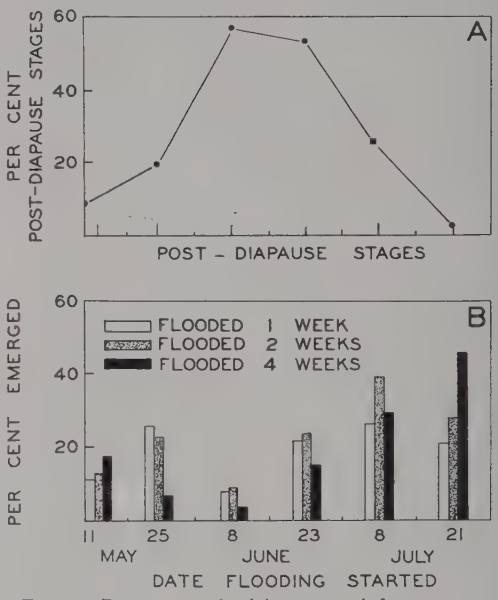

Fig. 3. Percentage of adults emerged from cocoons flooded for various periods at different times of the season (B) compared with incidence of post-diapause stages in untreated cocoons (A).

on June 8, for example, obviously contained a high proportion of susceptible post-diapause stages, resulting in severe mortality from the effect of flooding. The increased emergence following June 8 was caused by the progressively higher proportion of adults that emerged prior to flooding of those cages placed in water after June 8. This pre-treatment emergence makes up a progressively larger part of the total emergence shown in Figure 3B after June 8. Adults emerged from 26.8 per cent of the cocoons in two unflooded cages used as checks.

It is evident from these results that flooding for even one week during the critical period of post-diapause development can produce severe mortality in sawfly populations. Compared with the check cages, adult sawfly emergence from cocoons submerged on June 8 was reduced 70, 70, and 87 per cent for material submerged one, two, and four weeks respectively. Those submerged for four weeks on May 25 also experienced heavy mortality. The critical period will, of coruse, vary from year to year, depending on seasonal development.

Time and Duration of Emergence

This experiment was conducted in 1950 to determine the effect of several flooding treatments on the duration and period of emergence. Eight

standard cages each containing 200 overwintered cocoons were used. Two cages were left untreated in a well-drained location in the experimental plot to determine normal adult emergence. The remaining cages were submerged on June 8 as follows: two for one week, two for two weeks, and two for three weeks. Following immersion treatment the cages were removed to a well-drained location for adult emergence.

Emergence of adults was as follows:

Untreated check	23%
Flooded 1 week	6.4%
Flooded 2 weeks	6.0%
Flooded 3 weeks	4.1%

There was no significant difference in emergence between flooded cages, but emergence in all flooded cages was significantly lower than in the check.

Figure 4 shows the effect of treatment on the time and duration of adult emergence.

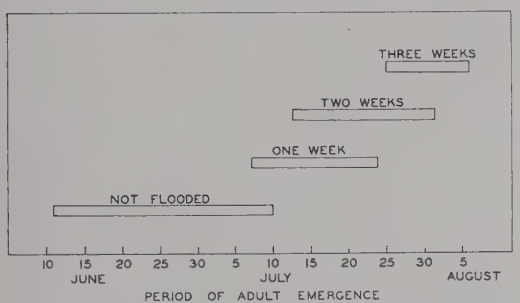

FIG. 4. Effect of three different periods of flooding on time and duration of adult emergence.

All flooding treatments delayed emergence markedly, the delay being roughly proportional to the duration of flooding. Besides reducing the percentage of emergence, flooding may affect the population adversely by retarding adult emergence. Usually the new terminal shoots of tamarack, in which the sawflies lay their eggs, begin to harden by about mid-July. It has been observed that many of these mature shoots are unsuitable for oviposition. Therefore, many sawfly adults that emerge after mid-July would have difficulty in finding suitable oviposition sites. Furthermore, many larvae hatching from eggs laid late in the season may not complete development before the onset of cool autumn weather or early frosts.

Newly Formed Cocoons

Cocoons for these experiments were gathered in July 1949, during the peak of the cocooning period. At time of collection cocoons were between one and two weeks old. Cocoons were prepared for the experiment in the same manner as overwintered cocoons. Using duplicate cages, cocoons of various ages were flooded for periods of one, two, and four weeks. Lots of cocoons 0-2, 2-4, 4-6, 6-8, and 8-10 weeks old were treated in this manner. As with the overwintered material, samples of 20 cocoons were removed from each cage and dissected immediately before flooding, and every two weeks following flooding until the ground was frozen. Mortalities recorded are shown in Table II. The table shows the average total mortality (including that caused by parasites, diseases, and other factors) for all post-treatment dissections. The average mortality of samples removed at two-week intervals from two untreated cages was 11 per cent.

TABLE II. *Average mortalities of larch sawfly larvae in cocoons before and after various periods of flooding*

Age of cocoons at time of flooding (weeks)	Percentage of larvae dead prior to flooding	Average percentage of larvae dead after flooding		
		Flooded 1 week	Flooded 2 weeks	Flooded 4 weeks
0-2	17.0	32.0	96.0	98.5
2-4	7.0	35.0	80.5	100.0
4-6	14.5	31.0	40.5	90.0
6-8	7.0	15.0*	24.0	62.5
8-10	10.0	7.5*	11.5*	22.5

*Mortalities not significantly different from pre-treatment mortality at the 5% level. All other values differ significantly from pre-treatment mortalities.

Table II shows that most larvae in cocoons less than four weeks old are killed by flooding for two weeks or more, and flooding for four weeks will kill most larvae in cocoons under six weeks old. Generally speaking, however, larvae in cocoons over four weeks old become progressively more resistant to flooding. Mortality of larvae in cocoons over six weeks old flooded for one week does not differ significantly from pre-treatment mortalities. The same applies to material over eight weeks old immersed for two weeks, and even flooding for four weeks causes mortality which is not much greater than in the pre-treatment samples. Larvae in cocoons eight to ten weeks old appear to have developed a degree of resistance to flooding somewhat greater than that found in diapause larvae in the spring. Under field conditions in Manitoba and Saskatchewan this degree of resistance is reached about mid-September. Flooding prior to that time would undoubtedly kill many larvae in cocoons.

There are indications that flooding may cause mortality for at least 6 weeks after cessation of treatment, and possibly longer. The pooled mor-

tality of cocoons up to six weeks old immediately following one week of flooding, and two, four and six weeks after flooding was calculated. The results are as follows:

Immediately following treatment	17%
Two weeks after treatment	27%
Four weeks after treatment	32%
Six weeks after treatment	37%

Immediately following treatment 17 per cent of the insects were dead, but six weeks later the mortality had increased to 37 per cent. The cumulative mortality rate appears to level off gradually and it would appear that very little additional mortality would occur as a result of flooding beyond six weeks after cessation of treatment. There was no evidence of similar cumulative mortality in untreated material.

To obtain more precise information on the period of flooding required to cause complete mortality, additional studies were carried out in 1950 with cocoons whose ages were known within two days.

Cocoons were divided into the following age classes for treatment; 0-1 week, 1-2 weeks, 2-3 weeks and 3-4 weeks. These were flooded under field conditions. Ten cocoons were removed from each lot daily to determine the percentage of mortality. The results are shown in Table III.

TABLE III. *Days required to produce 100% mortality in cocoons of various ages*

Age of cocoons in weeks	Days to cause 100% mortality
0-1	13
1-2	16
2-3	20
3-4	19
Overwintered	50*

*Approximate value derived from Figure 2.

It is clear from the table that resistance to flooding gradually increases with age. It is also quite evident that larvae in cocoons up to four weeks old are still highly susceptible to flooding, much more so than overwintered larvae in diapause.

Oxygen Consumption and Mortality

Flooding would seriously interfere with respiration processes, especially in phases where the oxygen demands are relatively high. Because of this it was considered probable that the rate of oxygen consumption of the various stages would be an important factor related to mortality from flooding. Studies were carried out on larvae in diapause, post-diapause stages in cocoons, mature uncocooned larvae, and newly cocooned larvae. The respirometer used was of the type described by Smith and Douglas (1949).

A series of trials was conducted during the summer of 1950 on mature larvae and newly formed cocoons. The average hourly rate of oxygen consumption per 100 mg. of insect wet-weight at 20° C. was determined. Readings were converted to standard temperature and pressure. The results are summarized in Table IV.

TABLE IV. *Oxygen consumption of full-grown and newly cocooned larvae*

Age in days	Insects measured	O_2 consumption μl/100 mg. wet wt./hr. at 20±2° C.*	Standard error
Full-grown larvae	20	85.98	±3.70
1-3	20	42.66	±1.58
6-8	28	10.45	±0.46
14	19	7.79	±0.46
21	20	5.70	±0.48
28	18	6.09	±0.38
35	20	6.87	±0.46

*At standard temperature and pressure.

These data show that the respiration rate of newly cocooned larvae is relatively high, though less than half the rate of fullgrown, uncocooned larvae. Soon after cocooning, however, the respiration rate begins to drop rapidly, and becomes more or less stabilized after about 14 days. Presumably it then continues at approximately the same level as could be expected for larvae in true diapause, as indicated by data to follow in Table V.

Comparing these results with mortality data in Tables II and III it appears that respiration rates are not directly proportional to resistance to flooding in new cocoons. Though the rate of oxygen consumption drops in two weeks to about the diapause level, many new cocoons less than six weeks old may be easily killed by flooding as indicated in Table II. Furthermore, this table shows that resistance to flooding develops more slowly than the decrease in respiration rates. However it is not improbable that rate of oxygen consumption is a primary function of tolerance to flooding, but in this experiment the true relationship may have been masked somewhat by differences in temperature between insects tested for oxygen consumption and insects submerged in the bog.

Another factor that may influence resistance to flooding is the presence in the cocoon wall of an inner layer relatively impervious to water. This inner layer makes up about half the thickness of the cocoon wall, and can be easily peeled from

the outer wall when the cocoon is wet. It is possible that the inner layer is relatively permeable in newly formed cocoons, and that permeability decreases with age. The importance of this layer in tolerance to flooding appears worthy of further investigation.

During the winter of 1949-50, respiration studies were conducted with diapause and post-diapause stages of the sawfly reared under laboratory conditions. The rates of oxygen consumption for the various stages recorded in these tests are shown in Table V. Unfortunately in this earlier work the rates were not related to insect weight and therefore they cannot be compared directly with data in Table IV. However, reasonably good comparisons can be assumed between Table IV and the data for eonymphs in Table V.

TABLE V. *Oxygen consumption of eonymphs, pronymphs, pupae, and adults of the larch sawfly (experiment conducted 20°-23°C.)*

Stage	Insects measured	O_2 consumption µl/hr. at S. T. P.	Standard error
Eonymphs	32	5.21	±0.39
Pronymphs	12	11.28	±0.96
Pupae	32	22.25	±1.62
Adults	5	50.75	±2.50

Comparison between Tables IV and V indicates that newly cocooned larvae at about two weeks of age have approximately the same rate of oxygen consumption as larvae in diapause, yet the larvae in diapause are much more resistant to flooding than larvae in newly formed cocoons two to four weeks old. However, for larvae in diapause and subsequent post-diapause developmental stages the ease with which insects may be killed by flooding appears to be related to the rate of oxygen consumption. A straight line relationship is indicated when the logarithms of the number of days' flooding required to produce 100 per cent mortality are plotted against the logarithms of the rate of oxygen consumption of eonymphs, pronymphs, pupae, and adults. The regression coefficient calculated from these data is significant beyond the 1 per cent level. The data are shown in Table VI.

TABLE VI. *Relation between period of flooding required to produce 100% mortality and oxygen consumption*

Stage	Days flooding to cause 100% mortality	Oxygen consumption 1 hr. S. T. P.
Eonymphs	50	5.21
Pronymphs	21	11.28
Pupae	7	22.25
Adults	2	50.75

Discussion

Results of experiments described indicate that larch sawfly larvae in cocoons in the state of diapause are highly resistant to flooding. However, there are two critical periods during which heavy mortality can be induced by relatively short periods of flooding. The first of these is in the spring, usually about mid-June in Manitoba and Saskatchewan. Then the majority of insects in the cocoons are in post-diapause stages of development and can be easily killed by flooding. Submergence for even a short period of one week will kill nearly all the insects in post-diapause stages that have not succumbed to other mortality factors. The second critical period is when the new cocoons are being formed, usually during the last two weeks of July and the first two weeks of August. New cocoons are easily killed by flooding and do not develop a high resistance to immersion until they are about eight weeks old. This stage of resistance is normally reached about mid-September. Flooding during other parts of the year, when insects are in the state of diapause, if sufficiently prolonged, will cause heavy mortality but the insects are then more resistant to moisture.

On a number of occasions it has been observed in tamarack bogs under study in Manitoba and Saskatchewan that excessive precipitation and high water levels in the spring and early summer do not produce expected decreases in larch sawfly populations. Owing to the high resistance of larvae in diapause to flooding, it is believed that water levels in the spring do not usually remain high long enough to kill many insects, unless flooding occurs during the period when post-diapause development is common. It is probable that sawfly populations are more frequently controlled or greatly reduced by flooding of new cocoons during late July and August.

Another aspect, which unfortunately could not be thoroughly analysed from the data available, is the question of delayed mortality that may take place for some time after flooding has ceased. It is suspected that a considerable proportion of larvae in cocoons not killed directly by "drowning" may die eventually as a result of flooding. This is not clearly indicated in results from experiments on overwintered insects in diapause, but reasonably conclusive evidence was obtained that larvae in new cocoons continue to die for at least six weeks after flooding has ceased. In fact, the final mortality six weeks after immersion ceased

was more than double the mortality recorded immediately after flooding for one week.

In the spring, when the insects are not killed by the immediate or delayed effects of flooding, emergence of the adults is retarded. Insects flooded for two or three weeks may emerge a month or more later than normal unflooded material. This in turn may affect adult oviposition adversely owing to the presence of hardened, mature, tamarack shoots unsuitable for egg laying.

Immediate, and possibly long-term population development may be influenced by the ground moisture content at the time larvae drop to spin cocoons. Where the moss cover is deep and the soil dry, larvae burrow more deeply into the moss to spin cocoons. When this happens they are in a more vulnerable and exposed position should excessive precipitation raise water levels before they emerge. On the other hand, if the soil is moist but not saturated, ideal cocooning conditions are provided and most larvae will spin cocoons nearer the surface where they are in a more favourable position to escape later flooding. Where the ground surface is saturated, with many open pools of water, probably few individuals that drop to spin cocoons survive. On numerous occasions it has been observed that in such situations innumerable larvae drop into the pools and drown. Furthermore most of those that are able to spin cocoons will probably not survive the excessive moisture.

This investigation shows that ground moisture is an important component of the environmental resistance of the larch sawfly. It is possible that the development and the decline of larch sawfly outbreaks are influenced strongly by precipitation cycles. This would appear to be a fruitful avenue of investigation.

Acknowledgments

Assistance on statistical analysis received from Mr. G. B. Oakland, Statistical Research and Service Unit, Science Service, is gratefully acknowledged. Valuable advice and constructive criticism were received from other members of the Forest Biology Laboratory, Winnipeg.

Summary

1. The peak occurrence of post-diapause stages of development in larch sawfly cocoons varies according to the season, but took place between June 8-25 in 1949 and June 15-30 in 1950.

2. During this period larch sawfly in cocoons may be easily killed by flooding. Almost complete mortality is caused by flooding for one week or more.

3. Overwintered eonymphs in diapause are highly resistant to flooding in the spring. About 50 days of flooding are needed to produce 100 per cent mortality. About 50 per cent may be killed by two weeks of immersion.

4. Post-diapause stages in cocoons are much more susceptible to flooding. One hundred per cent mortality is produced by flooding pronymphs for 21 days, pupae for seven days, and unemerged adults for two days.

5. The development of insects that survive flooding for one to three weeks is greatly retarded. Adults may emerge a month or more later than in unflooded material, the time being roughly proportional to the duration of immersion.

6. Newly formed cocoons up to four weeks old are highly susceptible to flooding for periods of two to four weeks. Cocoons over four weeks old become progressively more resistant to flooding, and at eight to ten weeks submergence for two weeks or less has no significant effect on mortality.

7. Short periods of flooding of new cocoons may not only kill insects immediately by drowning, but delayed mortality may occur for at least six weeks after flooding has ceased. It is not known how much delayed mortality can be attributed to overwintered cocoons that are flooded for short periods in the spring, but it is probably considerable.

8. While it is probably an important factor, the rate of oxygen consumption of newly cocooned larvae is not directly proportional to susceptibility to flooding. For overwintered eonymphs and post-diapause stages, susceptibility appears to be directly related to rate of oxygen consumption.

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COMPARISONS OF PROTECTED AND GRAZED MOUNTAIN RANGELANDS IN SOUTHWESTERN MONTANA

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Adequate management of any range cannot be achieved without a thorough understanding of the condition of vegetation and the trend in composition, vigor, and amount of cover. The application of condition and trend principles has consequently received increasing emphasis during the last decade (Humphrey 1949, Dyksterhuis 1949, and Ellison, *et al.* 1951). Factual data which relate the kind and rate of change to various grazing treatments, however, are scarce for most grassland types. Likewise, few comparisons have been made to ascertain objectively which responses are useful as criteria to guide range management. Perhaps as a consequence, evaluation of specific ranges has often been in terms of generalized concepts ("climax, subclimax, etc.") that might, but often do not, apply in a particular case. Also, for want of specific data, long-term successional trend concepts are too often applied to short-term management situations—a questionable process at best.

Hanson (1938, 1950) has reviewed the literature on grassland ecology, including grazing response, and Dyksterhuis (1949) has thoroughly treated the subject of range condition from the successional viewpoint. A brief review of the kinds of changes relative to grazing treatment is given here only to point up those most pertinent to this study.

Wright and Wright (1948) compared vegetal cover on protected and grazed ranges in south-central Montana. They reported that in the fescue type, Sandberg bluegrass (*Poa secunda*),[1] and certain shrubby species such as big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus nauseosus*), and snakeweed (*Gutierrezia sarothrae*) were more abundant under grazed conditions than in a non-grazed graveyard used for comparison. The possibility of fire having been an influence in the cemetery was not mentioned. Daubenmire (1940) classified bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*) as decreasers under grazing, while frequency of Sandberg bluegrass was considered as being scarcely affected, being neither an "increaser" nor a "decreaser." Pickford (1932) compared vegetation within exclosures to adjacent grazed areas in Utah. With prolonged heavy grazing, he found severe depletion of perennial grasses, an increase in sagebrush, and a decrease in total plant density, and occasionally an increase in density of perennial weeds and annual grasses. Mueggler (1950) concluded from a study in the upper Snake River plains that a "range in poor condition will improve very slowly if it is continually grazed in the spring at even a light stocking rate." Schwan, *et al.* (1949), working on a Kentucky bluegrass park in the ponderosa pine type in Colorado, found that protection from heavy grazing for four grazing seasons tripled herbage production compared to production on the adjacent heavily grazed area. They also showed that a good mulch cover favored greater herbage yield.

Somewhat in contrast to cover changes, studies of individual plants have shown that rather definite measurable and largely reproducible changes occur in certain individual plant characters in relation to herbage removal, either by grazing or clipping. Heady (1950) reported significant decreases in the basal area of bluebunch wheatgrass clumps relative to stubble height left after clipping. Under this treatment, height growth was correlated with clipping height. Blaisdell and Pechanec (1949) concluded that a decrease in height of bluebunch wheatgrass the year after clipping was not a sensitive indicator of vigor. However, they did find that time of herbage removal affected both herbage yield and height growth the following year. Daubenmire (1940) used stature and abundance of bluebunch wheatgrass plants as a means for classifying several areas in terms of severity of past grazing. Hanson and Stoddart (1940) compared protected and grazed beardless bluebunch wheatgrass (*Agropyron inerme*) and found protected plants 15.5 centimeters taller than those open to grazing. Research workers studying grazing response of other types of range have reported rather similar results. Hanson, *et al.* (1931) found in Colorado that western wheatgrass (*Agropyron smithii*) was shorter on continuously grazed than on deferred rotation pastures. Whitman and Helgeson (1946) in North Dakota, Weaver and Darland

[1] Species nomenclature in this paper is that of Kelsey and Dayton (1942).

(1947) in Nebraska, and Holscher (1945) in eastern Montana reported western wheatgrass plant heights and herbage yields decreased with clipping. In eastern Montana past heavy grazing reduced heights and yields of individual plants compared to lighter rates of past grazing.[2] Generally, findings of various workers indicate that herbage removal reduces plant vigor and herbage yields and results in certain compositional changes in range vegetation depending upon the severity of treatment.

The Idaho fescue-bluebunch wheatgrass type of southwestern Montana, grazed by thousands of cattle and sheep, is one of the important mountain range types. A better understanding of the condition and trend of the vegetation would result in more intelligent management of these ranges. The objective of this study was to compare the amount and composition of vegetal cover and individual plant height, size, and yield of important grasses on certain selected areas in this range type that were protected and that were open to cattle grazing. A special attempt was made to evaluate the observed responses in terms of their constancy, magnitude, and ease of measurement with a view to their possible use as management guides for the range administrator.

Description of Areas

The study was made during July and August in 1949 on the Beaverhead National Forest near the Vigilante Experimental Range in southwestern Montana. In this locale, Idaho fescue grows luxuriantly from about the 9,500-foot elevation on the better soils down to approximately 5,800 feet. Bluebunch wheatgrass is found at the lower elevation of this range and is not common above 7,200 feet.

Precipitation averages about 14 inches annually. About 60 to 70 per cent falls during the period April through September. Mean monthly precipitation is usually highest in June, averaging nearly 3 inches. Rainless periods of as much as 2 to 3 weeks' duration are common during the late summer months. Temperatures are generally favorable for plant growth from early May through August, although frosts may occur throughout the year. July, August, and early September are, however, usually frost-free. Maturity and dormancy are reached in August by most grasses. Additional moisture in the fall results in some regrowth, but the amount of herbage produced is usually of little grazing importance.

[2] Unpublished data on file at the Intermountain Forest and Range Experiment Station, Missoula, Montana.

The study or test areas, known locally as Lewis Creek, Lewis Creek Bench, Horse Pasture, Warm Springs, and Cottonwood, will be referred to hereafter as areas 1H, 2H, 3L, 4H, and 5M, respectively, to distinguish the areas and the intensity of their past use. Areas 1H, 2H, and 3L are on the west side of the Ruby River within one-half mile of each other, while 4H and 5M are about 3 miles away on the east side of the same drainage. All areas fall within a circle 1½ miles in radius. Average gradient is about 5 per cent with but small differences among the several areas. Elevations range from 6,400 to 7,100 feet above sea level. General views of two test areas are shown in Figure 1.

Fig. 1. Generalized views of grazed and protected parts of (A) area 1H, and (B) area 3L, near the Vigilante Experimental Range in southwestern Montana. Apparent difference in the amount of herbage inside and outside of exclosure in A is largely due to a difference in plant vigor and not current grazing.

Each of the study areas provided comparisons between grazed and protected ranges. Grazed portions have been open to domestic livestock for at least 50 years, while fenced exclosures have been maintained 15 to 18 years on areas 1H, 3L, 4H, and 5M, and 26 years on area 2H. Grazed portions of areas 1H, 2H, and 4H are believed to have received a heavy rate of use, area 5M a

more moderate rate, and 3L is known to have been grazed lightly (averaging about one animal month to each 9 acres per year between 1937 and 1949). Most of the grazing on areas 1H, 2H, and 4H has occurred during June and July, while 3L and 5M have, since about 1937, been grazed from June through the latter part of October. Protected portions of test areas 3L, 2H, 4H, 1H, and 5M, occupied ⅛, ¼, ¼, 2, and 125 acres, respectively. All open parts of the areas had received some grazing during the current year before observations were made.

Soil profiles of the various test areas were similar in most respects. Differences noted were greater between east- and west-facing slopes than within exposures. The easterly exposed areas 1H, 2H, and 3L had a 7-inch dark brown A horizon made up of very friable crumb aggregates less than ⅛ inch in diameter with weathered limestone fragments common, mild effervescence at 3 to 7 inches, and very abundant roots to 2 inches becoming moderately abundant at the 7-inch depth. A light brown B horizon composed of friable granular aggregates ⅛ to 1-½ inches in diameter extended from 7 to 12 inches with rock and rock fragments more common than in the A horizon, strong effervescence, and frequent roots. The C horizon, 12 inches downward, was more compact than B, still quite friable, contained heavily carbonated rocks, a very light brown in color interspersed with white streaks, and effervesced violently to a 24-inch depth. The working depth of roots was 16 inches on the grazed and 19 inches on the protected parts of the areas. The west-facing areas, 4H and 5M, differed mainly in that the soil was slightly deeper and less basic with greater root penetration. Soils of paired protected and grazed parts were similar except for usually more abundant roots at lower levels on the protected portions. Textural components derived by the hydrometer method (Bouyoucous 1928) were taken from the A horizon at each location. The respective sand, silt, and clay separates of test area soils were 43, 21, and 36 per cent for area 1H; 51, 28, and 21 per cent for area 2H; 63, 21, and 16 per cent for area 3L; 44, 16, and 40 per cent for area 4H; and 15, 17, and 68 per cent for area 5M. Based on the U.S.D.A. soil classification system, the respective textural classes of the test area soils were: area 1H, clay loam; 2H, sandy clay loam; 3L, rocky sandy loam; 4H, gravelly clay loam; and 5M, gravelly clay.

Primary forage grasses in the general area were Idaho fescue and bluebunch wheatgrass. The most common secondary grasses were thickspike wheatgrass (*Agropyron dasystachyum*), Sandberg bluegrass, Junegrass (*Koeleria cristata*) and plains reedgrass (*Calamagrostis montanensis*). Predominant perennial forbs included rose pussytoes (*Antennaria rosea*), Hood's phlox (*Phlox hoodii*), decumbent milkvetch (*Astragalus decumbens*), and trifid fleabane (*Erigeron trifidus*). The main shrubby species on the test areas were Douglas rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *lanceolatus*), fringed sagebrush (*Artemisia frigida*), and broom snakeweed, although big sagebrush and horsebrush (*Tetradymia canescens*) were also common elsewhere on these ranges.

In addition to these study areas, a limited supplementary comparison was made in 1950 on Cliff Lake Bench, an area which has never received more than very light sporadic use by domestic livestock. This bench is about 20 miles east of the test areas, at about 7,000 feet above mean sea level. Precipitation there averages higher and more of it occurs during the winter than at the Vigilante Station. Soils are porous and subject to very little runoff. Cover, area per clump, and height of Idaho fescue plants were compared on a small ridge and a nearby gentle slope.

Methods

Vegetation and soil characteristics compared on grazed and protected parts of the test areas included amount and composition of cover, ungrazed plant heights, number and size of individual plants of certain species; herbage production of dominant grasses; amount of surface litter; and rate of water absorption by the soils. Sampling was restricted to portions of the protected areas and adjacent grazed land, which, from the standpoint of slope, exposure, and soils, appeared reasonably comparable.

Vegetal cover and composition were observed on randomly located plots along mechanically spaced transects on a representative portion of each test area. With one exception, 30 or more 2 x 5 decimeter plots (1,000 square centimeters) were observed per treatment; *i.e.*, 30 plots in the portion of an area open to grazing use and 30 in its protected complement. The protected portion of area 3L was so small—⅛ acre—that only 15 plots could be well located there.

Estimates of cover 1 inch above ground level of each clump-forming species were made ocularly with the aid of a grid made up of 25 four-square centimeter units. The size of each clump was recorded separately. A clump was considered entire if the gaps within did not exceed 2 centimeters.

Single-stemmed species, such as plains reedgrass, were counted and converted to an area basis by arbitrarily considering 3 stems as providing 1 square centimeter of cover.

Height of about 30 ungrazed mature bluebunch wheatgrass and Idaho fescue plants were measured on each part of every test area where they occurred. An attempt was made to obtain the most common extended leaf height for each plant. Fruiting stalks, which were rare, were not measured. For the single-stemmed species, thickspike wheatgrass and plains reedgrass, the height of the tallest extended leaf was measured from tip to ground level. On the average, 150 stems of these species were measured on each part of the test areas on which they occurred.

Herbage yields of individual ungrazed clumps or stems per unit of area were obtained for the main forage grasses. An average of 30 individual plants of Idaho fescue and bluebunch wheatgrass were selected at random on each part of each test area, estimated for basal area, clipped ½ inch above the ground, sacked separately, and weighed after air drying. For the single-stemmed grasses, an average of 150 randomly selected stems per test area portion were clipped, composited by groups of 10, air dried and weighed. With these yield and cover data, yield per 0.1 meter plot of certain species was calculated.

Kind and amount of soil surface cover were measured on each sample plot by a modification of the point method of Levy and Madden (1933). Ten beads of solder affixed at 5-centimeter intervals along a wire stretched lengthwise through the center of the 2 x 5 decimeter frame provided sampling points immediately beneath the juncture of each solder bead and the wire. Points were classed as covered by dead plant material (including dung), by living vegetation, or as bare.

The rate of absorption of applied water by the soils of test areas 1H, 3L, 4H, and 5M was measured by the use of the tin can infiltrometer (Evanko 1950). An average of 30 trials was made on each part of each area. All plant material was removed from the ground surface at each sampling point, and one inch of water was applied and timed until disappearance. A second inch was immediately added to each setup and similarly timed.

The Cliff Lake Bench data were obtained from 30 2 x 5 decimeter plots and height measurements from 80 plants per site.

Cover of Grasses, Forbs, and Shrubs

Even though all test areas were in the same general range type, species frequency between areas varied considerably. Idaho fescue was most abundant on areas 3L, 4H, and 5M; Idaho fescue, thickspike wheatgrass, and plains reedgrass were co-dominants on area 2H; bluebunch wheatgrass provided the obvious aspect of area 1H but other common forage species were of almost equal importance. Sandberg bluegrass was abundant on all but area 3L.

Total grass cover on the grazed parts of areas 1H, 3L, 4H, and 5M was 14, 29, 26, and 12 per cent less, respectively, than on the protected counterparts (Table I). On three of these, the differences were statistically significant. The difference on area 2H was negligible. Data on individual species, however, did not usually reveal such clear-cut trends.

The effect of past treatment on Idaho fescue cover appeared to vary with its abundance. On areas 3L, 4H, and 5M, where this species was dominant, its cover was significantly less on the grazed parts. Differences between grazed and protected parts were not significant on areas 1H and 2H where it occurred only sparsely. The consistency of response on areas where Idaho fescue was definitely dominant suggests that it was here that this species was utilized most regularly and uniformly. The response of Idaho fescue may also have been influenced by differences in amounts and kinds of species with which it occurred. For example, on areas 1H and 2H, where no significant difference in Idaho fescue cover was noted between treatments, there was present a greater variety of grasses and more perennial forbs and shrubs than on the other areas.

The difficulty of assigning Idaho fescue a definite proportion of the total vegetal cover on this range type becomes apparent when cover composition of the protected areas is compared. Extreme variations in the amount of Idaho fescue were found between exclosures located in the same general range type. Comparing protected parts of areas 1H, 2H, and 3L, having similar exposure and presumably comparable in other respects, Idaho fescue was 91 and 84 per cent less abundant on areas 1H and 2H, respectively, than on area 3L. A comparison of Idaho fescue cover on the protected parts of these areas with that on the westerly exposed areas 4H and 5M reveals even greater differences. Inasmuch as length of protection had been similar for all exclosures, except area 2H, variation in Idaho fescue cover cannot be attributed to protection differences and must be a normal compositional variation occurring in this range type.

Further evidence showing that substantial variation in fescue abundance may be expected without

TABLE I. *Cover by species on protected and grazed (by cattle) parts of five test areas*

	Square centimeter cover per 0.1 M plot									
	Area 1H		Area 2H		Area 3L		Area 4H		Area 5M	
	Grazed	Protected	Grazed	Protected	Grazed	Protected	Grazed	Protected	Grazed	Protected
Grasses and sedges										
Agropyron dasystachium	9.5††	4.0	13.8	16.1	0.1	...	0.1	...	T*	
Agropyron spicatum	3.5††	12.8	...	2.2	2.6	1.1	0.9†	3.5	3.8	3.6
Calamagrostis montanensis	3.1	4.0	8.9††	15.2	14.8††	6.7	...	0.1		
Carex spp.	5.0	1.3	0.4	1.0	0.8	0.1	0.1	...	1.6	0.5
Festuca idahoensis	5.1	9.4	27.1	17.1	60.2††	107.01	88.4††	133.8	110.1††	156.1
Koeleria cristata	4.7	9.4	1.2	1.1	0.7	0.1	3.3††	0.4	5.8†	2.9
Poa secunda	24.0	21.8	36.9	32.1	3.7††	1.1	13.2††	5.2	33.4††	12.7
Others	...	1.0	0.6	2.0						
Total grasses and sedges	54.9	63.7	88.9	86.8	82.9†	116.2	106.0††	143.0	154.7†	175.8
Forbs										
Achillea lanulosa	...	0.2	1.6	1.4	0.3	...	2.2	1.9	0.6	1.0
Allium textile	0.1	0.2	...	...	...	0.1	...	...	0.4	
Antennaria rosea	...	1.7	18.0	2.5	2.9	3.9	13.5	14.1	29.5	27.2
Arenaria congesta	...	...	0.5	4.1	...	...	...	...	...	0.4
Aster spp.	0.2	1.3	14.3	14.7	0.7	...	...	...	0.2	0.1
Astragalus decumbens	7.0	6.6	2.7	2.7	2.4	0.5	0.8	2.1	5.5	3.5
Erigeron spp.	9.0	2.9	...	...	0.2	...	0.6	0.1	0.9	0.6
Erigeron trifidus	7.4†	18.7	...	...	2.0	0.3	5.2	1.2	0.2	T
Linum lewisi	0.9	2.1	...	...	0.1					
Oxytropis spp.	1.8	T	...	...	2.0	0.3				
Phlox hoodii	25.7	30.1	16.1	5.2	4.9	5.5	2.9	1.5	10.3	8.8
Potentilla gracilis ssp. *nuttalli*	1.1	0.4	1.2	1.8	...	...	0.4	T		
Solidago elongata	...	...	1.8	1.4	0.4	2.5	...	0.6		
Taraxacum officinale	0.5	0.7	23.3	14.9	0.2	...	0.4	...	0.1	0.2
Others	0.6	1.4	3.1	...	0.2	...	1.3	T	...	T
Total forbs	54.3	66.3	82.6	48.7	16.3	13.1	27.3	21.5	47.7	41.8
Shrubs										
Artemisia frigida	11.9	4.3	0.5	0.6	0.5	0.1	1.1	0.8	0.3	0.6
Artemisia tridentata	....	...	0.1	...	...	...	0.5			
Chrysothamnus viscidiflorus ssp. *lanceolatus*	1.7	0.5	5.5	5.2	1.2	2.5	0.6	0.6	1.8	0.9
Gutierrezia sarothrae	20.7	9.7	...	...	...	...	0.7			
Tetradymia canescens	0.3	0.4	0.8	0.2	1.6	0.7	...	0.5	0.6	0.2
Total shrubs	34.6†	14.9	6.9	6.0	3.3	3.3	2.9	1.9	2.7	1.7
Total all vegetation	143.8	144.9	178.4	141.5	102.5†	132.6	136.2	166.4	205.1	219.3

*Trace. †,††Differences between grazed and protected portions of individual areas statistically significant at 5 and 1 percent levels, respectively.

great differences in site was shown by the comparisons made of the near-pristine vegetation on Cliff Lake Bench. Average area occupied by Idaho fescue was 91 square centimeters per 2 x 5 decimeter plot on the small ridge, compared with 42 on the gentle slope. Percentage-wise this difference is greater than any which could be attributed to grazing treatment on the test areas.

Bluebunch wheatgrass might be considered the dominant or near dominant species only on area 1H. A comparison of protected and grazed parts of areas 1H, 2H, and 4H, where grazing use was considered heaviest, shows significantly less cover provided by this species on the grazed portions. On area 5M, where the grazed portion was used more conservatively, the amount of bluebunch wheatgrass cover was nearly equal on grazed and protected parts. However, more than twice as much cover was produced by this species on that portion of area 3L considered to have received light past grazing use. Despite its low abundance on all but area 1H, the observed differences suggest a definite response of bluebunch wheatgrass to grazing treatment. The variability of bluebunch wheatgrass abundance among sites and its scarcity over much of this range type means that abundance standards of this species as a criterion for evaluating range condition and trend must be closely associated with specific sites. No average, or range of allowable variation, seems meaningful for the type as a whole.

Thickspike wheatgrass appeared but slightly in-

fluenced by grazing or protection on areas 1H and 2H where it was a major component of the vegetal cover. On area 1H it was twice as abundant on the grazed part, but on area 2H it was about a fifth more abundant on the protected part. The conflicting differences cannot be assigned to variation in grazing intensity, for the grazed portions of both areas were considered to have been used similarly in the past. On the other test areas, thickspike wheatgrass was encountered only on the grazed portions.

Plains reedgrass was common only on areas 1H, 2H, and 3L. This species was about equally dense on protected and grazed portions of area 1H, significantly less so on the grazed than on the protected part of area 2H, and significantly more dense on the grazed part of area 3L. It is apparent that the various degrees of grazing use and total protection had little consistent effect on its abundance.

Sandberg bluegrass, unlike most other species, provided more cover on the grazed than on the protected portions of all test areas. The amount of difference was variable among areas. Basal area of this species on the grazed portions of areas 3L, 4H, and 5M was about 3 times as great as on the protected complements. Differences were relatively small and not significant on areas 1H and 2H. Where Sandberg bluegrass cover was significantly greater on the grazed portions of areas 3L, 4H, and 5M, Idaho fescue was significantly less abundant, suggesting an inverse relationship between these species.

Junegrass cover was significantly different between treatments only on areas 4H and 5M where it was greater on the grazed than on the protected portions. Kentucky bluegrass and big bluegrass were encountered in only small amounts on the protected portions of areas 1H and 2H, respectively. Sedge species were found on all areas but showed no consistent relationship to treatment. It was concluded that the data were too few to permit evaluation of the effects of grazing or protection on these minor species.

One annual forb, rockjasmine (*Androsace septentrionalis*), was found, and then only occasionally. Its presence did not appear to be associated with grazing or protection.

Total perennial forb cover was greater on the grazed than on the protected portions of all but test area 1H. A similar trend was shown by a group of generally distributed species which included rose pussytoes, Hoods phlox, decumbent milkvetch, and the fleabanes. Significantly, however, no single species was consistent with treatment. Nor did the number of species present vary consistently with grazing and protection. Therefore, it appears that only total cover provided by these perennial, and mostly unpalatable forbs, is sensitive enough to have some value as a condition and trend criterion.

Total cover provided by shrubby species was greater on the grazed than on the protected parts of all but test area 3L where it was equally abundant on both portions. As with forbs, while no individual shrubby species reflected treatment consistently, the group as a whole was generally favored by grazing.

Based on the data obtained in this study, variations in amount and composition of cover are normally so great that their use as range condition or trend criteria is unsatisfactory. The range in vegetation cover within exclosures was considerably greater than between grazed and protected vegetation on any one area. For example, while grass cover on protected areas ranged from 64 to 176 square centimeters per 2 x 5 decimeter plot, the maximum range between protected and grazed treatments of an area was only 37 square centimeters per plot. Similarly, compositional differences of vegetal cover assignable to treatment were generally less than differences among test areas. This applied to individual species as well as the grass, forb, and shrub groups. Such variations suggest that an exceedingly good knowledge of site influence is necessary to reliably predict vegetal cover and composition for a particular grazing treatment in this range type.

Size and Number of Plants

The number and size of Idaho fescue, bluebunch wheatgrass, and Sandberg bluegrass plants —the main clump-forming species on the test areas—appeared to have been affected by past grazing use and protection.

Table II. *Average size and number of Idaho fescue and bluebunch wheatgrass plants per plot on open and protected parts of test areas*

Species and test area	Area per clump (sq. cm.)		Clumps per plot (No.)	
	Grazed	Prot.	Grazed	Prot.
Idaho fescue				
Area 2H	6.4	6.7	4.3	2.2
Area 3L	5.4	6.4	11.5	13.7
Area 4H	3.5	6.9	22.6	19.8
Area 5M	4.3	7.4	22.0	17.9
Bluebunch wheatgrass				
Area 1H	3.7	8.0	0.8	2.1
Area 3L	2.8	2.9	1.1	1.1
Area 4H	1.2	1.8	0.5	1.6
Area 5M	1.7	2.2	2.0	1.5

Average basal area of individual Idaho fescue clumps, at the 1-inch level, was 5, 28, 49, and 42 per cent less on the grazed parts of areas 2H, 3L, 4H, and 5M, respectively, than that of clumps from their protected counterparts (Table II). Pocket gopher activity in the protected portion of area 2H was believed to have had some effect on plant size, thus reducing the observed differences. Excluding area 2H, the difference in size of clumps between grazed and protected parts of test areas was greatest, intermediate, and least for the respective open areas believed to have received heavy, conservative, and light past grazing use.

The usefulness and reliability of this character is further suggested by similarities in Idaho fescue clump basal areas among exclosures. Maximum average difference between clumps was but 1 square centimeter (6.4 to 7.4). Even near-pristine and otherwise favorable conditions resulted in clump basal areas of this species similar to those observed in the exclosures. This was shown by the observation that Idaho fescue clump area on Cliff Lake Bench averaged 6.4 square centimeters on the gentle slope and 7.9 on a nearby ridge.

Smaller average basal area of Idaho fescue clumps on grazed areas was apparently due to a general shift of the entire population toward smaller clumps. A higher proportion of small plants was found to occur on the grazed parts of all areas studied. From 5 to 9 per cent more plants in the 1 to 10 square centimeter basal area size class occurred on the grazed than on the protected portions. Plants larger than 10 square centimeters in area on the grazed parts ranged from 3 to 11 per cent of the total as compared with 12 to 16 on the protected portions. On Cliff Lake Bench, which was essentially ungrazed in the past, the percentage of plants larger than 10 square centimeters was 14 on the gentle slope and 20 on the ridge, further substantiating the general trend toward smaller Idaho fescue clumps under grazing as observed on the test areas.

While average basal area of Idaho fescue plants was less under grazed conditions, the number of plants was greatest on the grazed portions of 3 of the 4 test areas where this character was observed (Table II). Larger clumps, however, on the protected portions more than compensated for the fewer plants so that cover provided by this species was usually greater here than on the grazed parts. Excepting area 2H again, the number of Idaho fescue plants on the grazed parts appeared to be associated with degree of grazing use. The greatest number of plants occurred on the grazed part of area 4H, fewer were found on the more conservatively used part of area 5M, and the plants numbered least on the lightly grazed part of area 3L. Basal area of clumps, however, appears to be the more sensitive measure of response of Idaho fescue to varying levels of grazing use. One can probably deduce from this that with protection, Idaho fescue cover on the grazed portions would soon become similar to that in exclosures (Figure 2.).

Bluebunch wheatgrass was not as common as Idaho fescue on the test areas so the sample of this species is somewhat less adequate. However, size and number of bluebunch wheatgrass plants seemed to have been influenced by grazing treatment much as Idaho fescue (Table II). On all 4 of the test areas sampled, the average size of bluebunch wheatgrass plants was greater on the protected than on the grazed parts. Plants in the small size class, 1 to 5 square centimeters, were most numerous on the grazed parts of all test areas, ranging from 1 to 10 per cent more frequent than on the protected complements. Small average basal area of bluebunch wheatgrass is in part due to breaking down of clumps into units which, when separated by gaps of more than 2 centimeters, were classified as individual clumps. This breakdown was more common under grazing than protection. Unlike Idaho fescue, basal area of bluebunch wheatgrass clumps did not appear to be associated with the various levels of grazing use among the test areas. This may in part have been due to the clump classification used. There were usually more plants on the protected parts of the areas.

Without exception, Sandberg bluegrass plants were more numerous per unit area on the grazed than on the protected portions of all test areas. The number of plants on the grazed portions was about 3, 3, 2, 1.5, and 1.2 times greater than on the protected portions of areas 3L, 5M, 4H, 1H, and 2H, respectively. While average clump area of Sandberg bluegrass ranged from 1.2 to 4.1 square centimeters between test areas, size differences between grazed and protected portions of each test area were small and inconsistent. Thus, unlike Idaho fescue and bluebunch wheatgrass, differences in Sandberg bluegrass cover between grazed and protected portions were accounted for largely by a difference in number of plants, rather than size of individuals.

Other clump-forming species were not abundant enough to merit analysis relative to number and size of clumps.

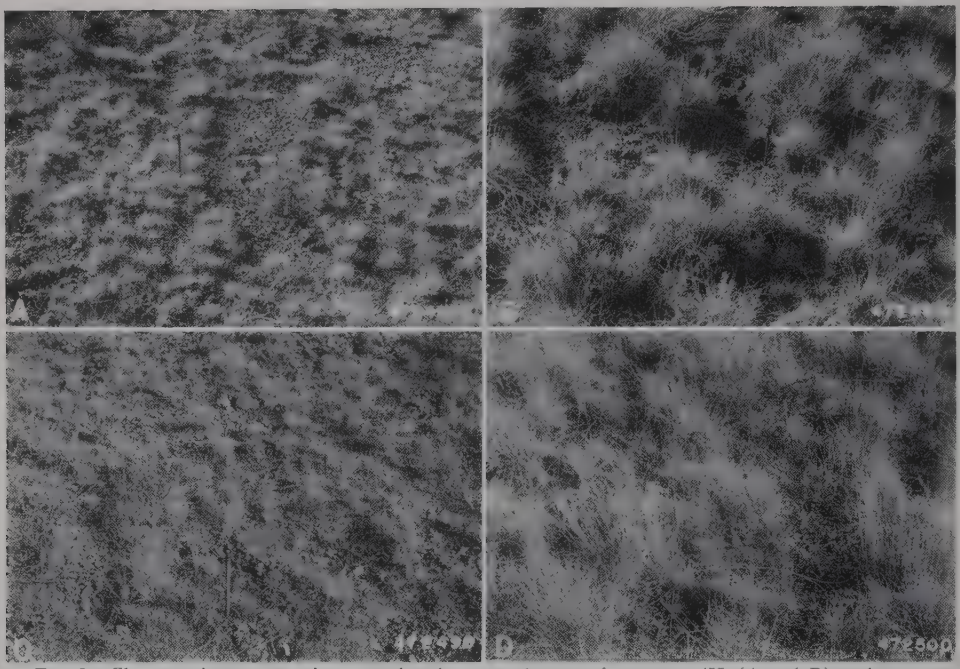

FIG. 2. Close-up views contrasting grazed and protected parts of test area 4H (A and B) and test area 5M (C and D). The main species represented are Idaho fescue and bluebunch wheatgrass. While vegetal cover was somewhat less on the grazed portions, the most important differences were in basal area, height, and yield of individual plants. Erosion pavement was more conspicuous on grazed portions but was also present under protection.

MATURE HEIGHTS

Mature leaf height of all major grasses measured on each area was invariably less on the grazed portions (Table III). Differences ranged from 13 to 54 per cent and appeared to be roughly proportional to intensity of past grazing use. Idaho fescue, for example, probably received the heaviest use. It also had the greatest percentage spread between heights on grazed and protected portions. On the other end of the scale was plains reedgrass. Grazed lightly, it showed the smallest percentage height differential. Likewise, all species measured on area 3L, known to have been grazed lightly for several years, showed a substantially smaller spread than was found on any other area. In general, there was close similarity of average leaf heights of individuals of a particular species among exclosures. The range for Idaho fescue was only 0.4 centimeter (6.6 to 7.0). On Cliff Lake Bench, however, the difference on the two sites was about 25 per cent. Average height in this more favorable environment was almost twice as great as on the protected portions of the test areas. This shows that site, season, and other conditions need to be considered

TABLE III. *Height and weight of individual plants, yield per square centimeter, and calculated yield per plot of four grass species on open and protected areas*

Species and test area	Height (cm.)		Yield per clump or group‡ (grams)		Yield per sq. cm. of basal area (grams)		Yield per 2 × 5 dm. plot** (grams)	
	Grazed	Prot.	Grazed	Prot.	Grazed	Prot.	Grazed	Prot.
Idaho fescue								
Area 2H....	3.2†	7.0	0.20†	0.60	0.03	0.06	0.81	1.03
Area 3L....	5.4	6.8	0.39	0.47	0.05	0.06	3.01	6.43
Area 4H....	3.2†	6.6	0.13†	0.58	0.03	0.05	2.65	6.69
Area 5M....	3.8†	6.9	0.20†	0.64	0.03	0.05	3.30	7.80
Bluebunch wheatgrass								
Area 1H....	8.8†	16.1	0.24†	2.02	0.06	0.14	0.21	1.79
Area 3L....	15.2*	17.4	0.28	0.34	0.17	0.16	0.44	0.19
Area 5M....	10.8*	18.9	0.23	0.61	0.12	0.18	0.46	0.65
Thickspike wheatgrass								
Area 1H....	10.8†	14.8	0.28†	0.53	0.08	0.16	0.76	0.64
Area 2H....	10.2†	18.3	0.23†	0.57	0.07	0.17	0.97	2.74
Plains reedgrass								
Area 1H....	14.3†	18.4	0.40†	0.53	0.12	0.16	0.37	0.64
Area 2H....	11.3†	17.4	0.25†	0.43	0.08	0.13	0.71	1.98
Area 3L....	12.4†	14.2	0.26	0.33	0.08	0.10	1.18	0.67

‡Weight of 10 stems for thickspike wheatgrass and plains reedgrass.
**Yield in grams per plot may be converted to pounds per acre by multiplying by 89.14.
†Significantly different at the 1 per cent level.
*Significantly different at the 5 per cent level.

in using this rather sensitive character to evaluate the effects of past grazing use.

Herbage Yield

Yield of palatable herbage is the summary measurement of the effect of range treatment on vegetation. While in this study herbage yield was restricted to the dominant grasses—Idaho fescue, bluebunch wheatgrass, thickspike wheatgrass, and plains reedgrass—the data secured probably reflect with reasonable accuracy the relative amounts of herbage useful to livestock.

Of the 4 grasses considered, herbage produced per clump or group of stems when clipped ½ inch above the ground ranged from 17 to 88 per cent less on the grazed than on the protected portions of the test areas (Table III). The greater yield of Idaho fescue and bluebunch wheatgrass clumps on the protected parts corresponded with greater height and larger basal area of those plants. With the single-stemmed species—thickspike wheatgrass and plains reedgrass—yield differences per group of 10 stems were similar to leaf height differences between protected and grazed plants. However, on any particular area, weight differentials expressed as a percentage were invariably greater than those of height, suggesting that other reductions besides height were involved. These may have included thickness of stems and size and number of individual leaves. In 8 of the 12 comparisons made on a clump or group basis, yield differences were significant.

Excepting bluebunch wheatgrass on area 3L, yield per square centimeter of basal area supplied by each of the 4 grasses observed was also less on the grazed than on the protected parts of the test areas. Again the greater yield of protected plants could be largely explained by their height advantage over the plants that were open to grazing. Production on the grazed parts compared to that on the protected parts of areas on which the grasses were measured was as follows, when yields per square centimeter were used: 17 to 50 per cent less for Idaho fescue, 0 to 57 per cent less for bluebunch wheatgrass, 50 to 59 per cent less for thickspike wheatgrass, and 20 to 38 per cent less for plains reedgrass. Production per square centimeter of Idaho fescue and bluebunch wheatgrass appeared to be directly related to intensity of grazing use. On those areas that were considered heavily used in the past, these species produced about half the herbage obtained from the protected parts. With more conservative use, yield was about two-thirds that of protected parts and almost equal where light past grazing had been practiced.

Response of thickspike wheatgrass and plains reedgrass to past grazing levels could not be judged since all grazing rates were not represented. However, the least difference again occurred on area 3L.

Yields of important grass species are shown in the last column of Table III. These figures were calculated by multiplying yield per square centimeter of basal area (Table II) by the square centimeters occupied per plot (Table I) and thus reflect differences in cover as well as vigor of individual plants. Although, as a general rule, yields were higher under protection, there were exceptions for all species but Idaho fescue. These exceptions point up the fact that greater ground cover may counteract or completely obscure important differences in plant vigor definitely assignable to grazing treatments. Therefore, yield alone of individual species may not give a reliable measure of range condition.

Surface Litter

Effects of protection and past grazing use were further reflected in the amount of litter accumulated on the ground surface. There was more surface litter on interspaces of the protected portions of all areas than on the corresponding grazed parts. The protected parts of areas 1H, 2H, 3L, 4H, and 5M had 21.8, 13.8, 7.1, 10.5, and 26.1 per cent more litter, respectively, than the portions that were grazed. This difference was significant on 3 of the 5 areas. Conversely, more bare ground was exposed consistently on the grazed portions because of the smaller amount of living vegetation as well as less dead material. Differences in the amount of bare ground between grazed and protected parts of areas were 20.3, 10.9, 6.8, 13.4, and 18.6 per cent for areas 1H, 2H, 3L, 4H, and 5M, respectively. The unusually high litter cover and low amount of bare ground on both parts of areas 2H and 3L were due to an abundance of mostly dead Selaginella (*Selaginella* sp.) at those locations. The variation in litter and bare area within treatments among areas indicates the difficulty of using this factor to evaluate the effects of grazing treatment without taking into account individual sites. Runoff, slope, exposure, and amount and kind of vegetation of all appear to influence the amount of litter occupying interspaces of this mountain type.

Water Absorption

Although tests made with tin can infiltrometers are not precise, they do give a relative measure of surface soil permeability. The ability of the test area soils to absorb artificially applied water, as indicated by such tests, was apparently related

to observed differences in vegetal cover and amounts of bare ground and litter between grazed and protected portions. Average rate of water absorption was less on the grazed than on the protected portions of areas 1H, 3L, 4H, and 5M (Figure 3). Area 2H was not sampled. Time required for the absorption of 1 inch of water on the grazed parts of the test areas ranged from 6 to 78 per cent longer than on the protected portions. Excluding area 3L, where the small difference is attributed to the light grazing practiced there over the past 17 years, the grazed parts required an average of about 1.5 times longer to absorb the first inch of water than did the protected parts. Similar results were experienced when the second inch of water was applied.

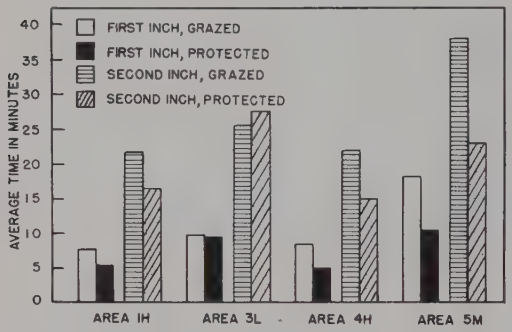

FIG. 3. Average time in minutes required for the disappearance of first and second inches of artificially applied water on protected and grazed parts of test areas.

Unpublished results of studies made near Miles City, Montana, show a decrease in absorption rate to be associated with an increase in soil volume-weight and a decrease in soil noncapillary pore space. It is likely that the same process has occurred in the soils tested here.

DISCUSSION

Inasmuch as the areas that have been referred to as protected had received grazing use for several years prior to exclosure establishment, differences between treatments must not be taken as a comparison between virgin and used range. Rather they are essentially expressions of the direction in which modifications have taken place since the establishment of exclosures.

Small exclosures may, especially by increasing snow accumulation, modify the local environment and the vegetation entirely apart from differences due to grazing treatment (Daubenmire 1940). This situation, if operative, would improve the plant environment in the exclosures over the outside inasmuch as moisture is the primary limiting factor to plant growth in the study area.

Thus, one would expect a magnification of differences between protection and grazing treatments. Lack of substantial difference of any particular character measured would, under these circumstances, be strong evidence against its general usefulness in range evaluation. There was, however, little evidence that size of exclosures in this study significantly influenced results. Differences measured were as great (or as small) on the area with the largest exclosure as on that with the smallest. Attraction of rodents to small exclosures may also upset validity of comparisons. Only on area 2H, however, was any excessive rodent action observed and here the net effect was of questionable significance.

In evaluating response of protected versus grazed range, primary considerations are given to (1) constancy of response, (2) magnitude of response, and (3) ease of measurement. The last is, of course, largely a function of the other two.

Some of the vegetal characters measured appeared to reflect treatment more consistently and with greater magnitude than others. Those were measurements descriptive of individual plants: height, basal area, and weight of top growth. On the other hand, measurements of relationships among species and area occupied by individuals or groups of species varied widely among areas within treatments, reflected treatment irregularly, and were difficult to measure. Even Sandberg bluegrass, which showed consistently higher abundance on the grazed portion of each area, varied vastly within treatments among the 5 test areas.

It is apparent that, whether grazed or not, the plants successfully maintained a comparatively closed community. Had grazing previous to or after exclosure establishment been severe enough to cause actual denudation, thereby opening the communities, differences between protected and open portions in amount and kind of cover and in distribution probably would have been substantially greater. The practical impossibility of establishing seedlings through artificial reseeding on uncultivated rangeland, except when excessive deterioration has taken place, supports this contention.

Without persistent patterns of composition and cover relationships among the several areas, it is not possible to set up reliable cover criteria for this range type. Furthermore, the lack of evidence of substantial cover modifications after 15 to 28 years' protection or continued grazing shows

that succession under these conditions has proceeded at a snail's pace or did not occur. In any case, it is evident that before cover and distribution measurements can be accepted as useful and valid criteria of management on this type, much more must be learned about the relationship between these elements and site, and about the effect of site on the rate at which changes are likely to occur given a certain treatment.

As previously pointed out, measurements of individual plant characteristics show a comparatively high degree of constancy and association with treatment. Average heights of Idaho fescue leafage among exclosures ranged between 6.6 and 7.0 centimeters, grams per clump between 0.47 and 0.64, and grams per square centimeter of basal area between 0.05 and 0.06. In no case did measurements of individual Idaho fescue plant characters on any grazed area exceed those of plants within any exclosure. In other words, differences between grazing and protection were greater than differences assignable to site. Furthermore, where actual treatments were but slightly different, as in the case of area 3L, differences in plant response were small and insignificant. A similar relationship was shown for bluebunch wheatgrass, except that yield per clump deviated. Measurements of individual characteristics of thickspike wheatgrass and plains reedgrass vacillated more but similar trends were indicated. Under conditions of dominance, or near dominance, response would probably be more uniform.

While associated with treatment, litter cover varied so much among areas that had been protected or grazed similarly that its application in evaluation of range condition on this type would at this stage have to be made with great discretion—except on a specific site basis. The same rule applies to rate of water absorption by soils. In the case of water absorption, however, it would seem possible to correlate eventually absorption rate with physical characteristics of soils so that a standard could be developed, based on certain measurable soil characteristics.

Certain recommendations seem in order for using measurements of individual plants along with exclosures to evaluate range condition or effects of grazing treatment. It is apparent that on this range type wide and important differences exist among sites. Largely due to these wide differences—which are probably not peculiar to the Vigilante range—it follows that standards of comparison must be chosen so that one may be assured that observed differences can be attributed to the grazing factor. Exclosures probably provide better means than any other readily available for assuring validity of comparisons. To serve optimally, exclosures need to be carefully located relative to significant site, vegetation, and grazing variations. Where possible they should also be large enough to permit full scope for natural processes (Hanson 1938). However, as has been indicated, many valid and highly useful comparisons can be made between small exclosures and adjacent areas open to grazing.

Cover changes may occur but are likely to be very slow whenever a relatively closed community is maintained. Therefore, from the standpoint of practical range management, probably the more immediately useful information will come from measurements which reflect vigor of the important forage species. Vigor responses are probably not only most easily measured and specific but also occur sooner than fundamental changes in interspecies relationships. This sensitiveness to treatment is of prime importance for, as stated by Hanson (1950), "Recognition of the first signs of reduced vitality is most important in the management of grasslands because something can often be done to change the trend before it is too late." Furthermore, even when amount and composition of cover should and can be improved, about all that can be done in most situations is to change grazing management so as to raise the vigor of the desired species to a high level. Then the stage is set for maximum seed production and the high competitive capacity necessary for the replacement by natural processes of less adapted species by those which have been depleted by over use.

Summary

Comparisons of 5 areas, each with parts open to and protected from grazing, were made in the Idaho fescue-bluebunch wheatgrass type in southwestern Montana. Various elements of the vegetation and water absorption by the soils were measured to determine effects of grazing and protection treatments. Measurements which could have been affected directly by current grazing, such a height growth and yield, were restricted to ungrazed plants. Detailed findings from the study were:

1. While all test areas were located within a 1½-mile radius of each other, composition of vegetal cover within and outside the exclosures varied substantially among areas.

2. The following trends were observed in vegetation cover relative to treatment:

a. Unpalatable forbs and shrubs were more common on the grazed than on protected counterparts. Differences were small but consistent.

No particular species appeared to stand out as having high indicator value.

b. Total grass cover was slightly greater on the protected than on the grazed portions. Idaho fescue provided less cover on the grazed portions of those areas where it was dominant. Bluebunch wheatgrass showed a similar but less pronounced trend. Only Sandberg bluegrass was persistently most abundant on the parts of the areas open to grazing.

c. Variations were so great among areas that no common compositional pattern could be defined for the type.

3. Leaf heights, basal area per clump, and herbage yield per plant and per square centimeter for the major forage species were, with one exception, greatest on the protected portions in each of these comparisons. Comparatively close correspondence of these characteristics existed within treatments among areas, especially for Idaho fescue and bluebunch wheatgrass.

4. Calculated yield of the most common forage species was usually greatest on the protected areas.

5. Litter on the soil surface and rate of water absorption by the soil were, in most cases, substantially less on the grazed portion of the areas. They varied considerably between areas within treatments.

6. In a comparison between a lightly used and a protected area, amount and kind of cover and frequency of plant occurrence did not reflect the light use. Measurements of height, clump basal area, yield per clump, and yield per square centimeter showed less difference in this comparison than where protected and more heavily grazed areas were compared.

On this mountain bunchgrass type, it was found that leaf height, plant area, and yield per clump and unit of plant area of individuals of important forage species appear to furnish more reliable and usable criteria for evaluating range condition than do cover estimates. Strategically located exclosures may provide the range administrator with a standard for evaluating, in a relatively simple manner, the degree to which the grazing treatment has affected certain characters, especially those associated with vigor of plants.

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STUDIES ON *MESODON FERRISSI* (GASTROPODA, PULMONATA)
I. GENERAL ECOLOGY AND BIOMETRIC ANALYSIS

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INTRODUCTION

While the study of ecological variation in American freshwater mollusks has been pursued by a number of workers, there has been but little work done on ecologic variation in land mollusks. A few people—Cockerell (1903), Walker (1910), Foster (1936a, 1936b) and Archer (1948)—have applied statistical analysis to variation in land mollusks, but I know of no attempt to correlate variation with ecology, or to undertake the statistical analysis of the variation of a species over its entire range. In a series of papers, of which this is the first, I hope to carry out a survey of one species, *Mesodon ferrissi,* in relation to ecologic, altitudinal and geographic factors.

Considerable intraspecific variation occurs in land mollusks and molluscan taxonomy is thoroughly burdened with named ecologic variants. Lack of statistical treatment of variation is partially caused by the impossibility of satisfactorily expressing color shade and details of sculpture or thickness of shell mathematically, but perhaps mainly through lack of large series of specimens with ecologic data. Boycott (1928) has demonstrated possible uses of statistics in studying molluscan variation and Alkins (1928) has used statistical analysis in delineating two species, but I know of no similar American work.

Mesodon ferrissi has been chosen for this study for several reasons. In the first place, it is a highly isolated species with no close relatives known. It has a fairly large shell which can be measured with some degree of accuracy. It has a very limited geographic range, which will permit the entire population of the species to be sampled. Within its area it seems to be broken up into small population units which are presumably isolated so that the effects of ecologic variation coupled with genetic drift can be studied. It probably has a narrow range of tolerance of ecologic conditions. Previous collecting has shown that individuals are abundant, although the former inaccessibility of the region has caused it to be long considered a rare species. To as much extent as any area of the United States, its home range has been relatively unaffected by man so that it represents a species under natural conditions rather than one adapting to the changed environment caused by human habitation. In addition it has the great asset of developing a reflected lip and ceasing growth at maturity, so it becomes possible to eliminate measuring error caused by age differences.

This report is based upon some personal observations, previous contributions on *Mesodon ferrissi* and a statistical analysis of 260 specimens. Its primary function is to indicate the intended lines of research and to stimulate interest along similar lines in others.

For permission to examine specimens in their care, I wish to thank Dr. Fritz Haas, Dr. Henry van der Schalie, Dr. Henry A. Pilsbry, Dr. William J. Clench, Dr. Harold Rehder and Phil Marsh. Acknowledgment is made to Dr. Herndon Dowling, Dr. Henry van der Schalie, and Dr. Francis Evans for many helpful suggestions. A special note of thinks is given to Glenn R. Webb for the gift of three live adults.

Taxonomic Position

Pilsbry (1940) revised the polygyrid snails, basing a great deal of his work on the visceral anatomy. On the basis of his studies, *Mesodon ferrissi* is an isolated species. While superficially similar to *Triodopsis dentifera* in shell characters, it is readily separable from that species by sculpture and genitalia. In the examined material I have seen two cases of *Mesodon perigraptus* (Pilsbry) being mistaken for *ferrissi,* but no other known snail could be confused with it.

Up to the present typical *ferrissi* and a subspecies, *M. f. sericeus* (Ferriss), of dubious validity and uncertain locality have been described. Pilsbry (1940: 738) has fully covered the problem of *sericeus* and its repetition at this point is unnecessary.

HISTORICAL SUMMARY

Mesodon ferrissi was described by Pilsbry (1897) from specimens collected by James H. Ferriss on a trip through the Smoky Mountains during the summer of 1897. The specimens were collected on the trail from Mirey Ridge to Clingmans Dome (see map, Fig. 1). The holotype and seven paratypes are ANSP 72332 and two paratypes labeled "Mirey Ridge" are UMMZ 97253. Probably other paratypic specimens are scattered

through old collections, but I have seen no others labeled type material.

Most of the known specimens date from a trip taken in July and August 1899 by Bryant Walker, George F. Clapp, H. E. Sargent, H. A. Pilsbry and J. H. Ferriss. Both Pilsbry (1900) and Ferriss (1900) have given résumés of this trip. From Cades Cove the party packed in to Thunderhead and after a few days there followed the trail (now the famous Appalachian Trail) to Mirey Ridge, then over Silers Bald to Clingmans Dome (Fig. 1). Sargent and Ferriss left the main party to go to Andrews Bald, then retraced their steps to Clingmans Dome and Silers Bald to follow the Welch Bald Trail into North Carolina. *M. ferrissi* was found on Andrews Bald ("we got over 80 *Polygyra ferrissi* each"), Mirey Ridge, Clingmans Dome, Silers Bald and Welch Bald ("three specimens in two days"). Ferriss made several further trips to the Smokies and collected *Mesodon ferrissi* as far north as Mt. Guyot. Subsequent collecting, notably by Clench and Archer, added Mt. Collins, Mt. LeConte, Indian Gap, New Found Gap, the Chimneys and other points in that general area to the known distribution. The paving of Tennessee Route Number 71 and the addition of the road to Clingmans Dome has enabled several private collectors to obtain lots recently.

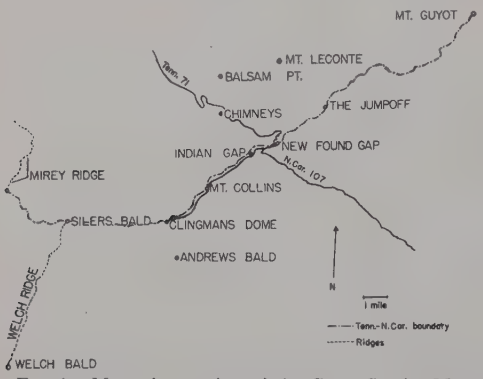

FIG. 1. Map of a section of the Great Smoky Mountains, Tennessee and North Carolina, showing localities mentioned.

Range

From the original collections, *M. ferrissi* was known from an area covered by an equilateral triangle cornered by Welch Bald, Mirey Ridge and Clingmans Dome. As predicted by Pilsbry (1900: 116), further collecting extended its range along the interstate mountain ridge to Mt. Guyot. The area below Mirey Ridge near Thunderhead and Cades Cove has been fairly completely explored by conchologists and it is doubtful if *M. ferrissi* will be found south of Mirey Ridge. The exact northern limits are as yet uncertain. If Pilsbry's location of the type locality of *M. ferrissi sericeus* on Plott Balsam in Jackson Co., North Carolina (ca. 35° 26′ North, 83° 10′ West) is correct, the range will be extended. Regardless of the locality of *sericeus, M. ferrissi* turns out to have a highly restricted range for a polygyrid snail. In altitude, *M. ferrissi* ranges from the base of the Chimneys (2800′) to the summit of Clingmans Dome (6600′). The exact lower limit is uncertain, but will probably not go below 2500 ft.

Ecology

Present knowledge of the ecology of this species rests upon information gathered at the turn of the century by Pilsbry and Ferriss, some notes by Clench and a few observations made by the author in 1950. The known data are very limited and apply to only a few localities.

The ecology of *Mesodon ferrissi* is closely connected with the geology of the area. The mountains consist of massive beds of conglomerate rocks dipping sharply to the south and southeast. The north and northwest slopes are quite precipitous and strewn with rocks broken off from the exposed edges of the strata. Many rock ledges and boulders have part of the undersurface free of the ground. The exposed area is covered with a luxuriant growth of fungi and a film of seepage water. The ground is covered with sphagnum moss and many rotting logs.

On Clingmans Dome and Andrews Bald *Mesodon ferrissi* is found on the undersurface of overhanging rocks, presumably feeding on the fungi. Generally it is solitary or found in groups of two or three individuals. However, Ferriss (1900: 51) reports as many as eight specimens per rock from Andrews Bald and says that occasionally *Mesodon clarki, Mesodon andrewsi altivaga, Stenotrema depilatum, Paravitrea lamellidens* and *Paravitrea clappi* are found on the same rock, "but not often." On the northwest slope of Clingmans Dome the author observed a number of specimens on the undersurfaces of rocks, and one specimen crawling over a wet rock in the open. Although Pilsbry reported a few specimens from the summit of Clingmans Dome, personal observations seemed to relegate that area to the peculiar *Vitrinizonites*. Conditions on Mirey Ridge are almost the same (Pilsbry 1900: 121).

A highly interesting and important find is that of Clench in collecting *M. ferrissi* at the base of the Chimneys "mainly on small moss covered rocks on a steep slope with plenty of seepage water" (Clench 1937: 18). This locality has been

subsequently visited by at least two other collectors Leslie Hubricht and Glenn R. Webb. An additional locality with ecologic data is a small rock slide about ¾ mile below New Found Gap at about 4800 ft. altitude. The rocks were very tightly packed and there was a continual flow of water over the pile. Several young specimens were observed and two dead adults were taken by the author.

Boycott (1929, 1934) has quite adequately summarized the ecological requirements of land mollusks. The main limiting factors are those of shelter, lime and moisture. Food cannot be considered a limiting factor as snails will generally feed on any decaying matter. Because of this, the relation of molluscan distribution to plant communities should be considered in the light of physico-chemical criteria: availability of lime, shelter, and the retention of moisture during dry spells. To the extent that the above conditions are determined by the plant community, the relation between snails and plants is direct, but it is a fallacy to consider that it is the plant community, *per se,* rather than physical conditions which determine molluscan distribution. Studies on molluscan ecology should be directed towards study of the above factors rather than to occurrence in a particular plant community.

With the above criteria in mind, it becomes possible to indicate several possible points concerning the exact ecology of *Mesodon ferrissi.* The most striking fact is the extreme moisture in which it lives. All reported localities are areas with actual flow of seepage water. This is a remarkably moist situation for a polygyrid snail and I know no other member of the family which will tolerate a constant flow of water over the microhabitat. As Glenn R. Webb reports (personal communication) and my own observations confirm, *M. ferrissi* is extremely susceptible to moderate periods of dryness in the vivarium. It probably is restricted to areas of excessive moisture in its native habitat. The combination of seepage water and rocks is mentioned in every report. As indicated by Ferriss, it seems to occupy a peculiar niche only rarely invaded by other snails.

The above summary leaves much to be filled in, but the key items of rocks and seepage water appear to be the important aspects of its ecology.

Material and Methods

Specimens of *Mesodon ferrissi* in the Academy of Natural Sciences of Philadelphia, United States National Museum, Museum of Comparative Zoology, Chicago Natural History Museum, University of Michigan Museum of Zoology, P. L. Marsh and the author's collection were examined. With a most welcome gift of three living adults from Glenn R. Webb, a total of 260 specimens was seen.

From early accounts, probably at least another 100 specimens of the Pilsbry, Ferriss, Walker, Clapp and Sargent material are scattered through old collections. As was (and still is) customary, the great majority of large series was traded to other conchologists in driblets of twos or threes, so that the original Ferriss-Sargent material has probably been split into thirty or forty lots and is scattered throughout the entire world. Many of these small segments have gravitated into large collections. Without seeing either the Ferriss or Sargent collections, I located fifty-five of their Andrews Bald specimens in the larger collections mentioned above. Within recent years at least another seventy-five specimens have been collected by many individuals.

The height and diameter of all specimens were measured with a vernier caliper to the nearest 0.1 mm. These measurements were made according to the method of Pilsbry (1939: xi) rather than Boycott (1928: 28). In addition careful whorl counts were made on the 133 specimens in the UMMZ, Marsh and author's collections to the nearest one-eighth whorl.

To test the accuracy of the measurements, the 133 specimens immediately available were measured on three separate occasions and the results compared. In only eight cases did the diameter vary more than 0.2 mm. Measurement of the height was, as expected, less accurate because of the error inherent in judging the angle at which to place the specimen between the jaws of the caliper when measuring. In one case the range of difference was 0.4 mm. In all cases of variation of 0.3 mm., a series of seven measurements were taken and the median selected. Whorl count was usually the same and did not vary more than one-eighth whorl.

The height-diameter ratio (abbreviated h/d ratio) was computed and several simple statistical tests were applied to the entire sample. The tests employed are essentially those used by Boycott (1928) as modified by recent changes in statistical methods.

An attempt was made to break the large sample into smaller ones based on natural populations from small geographic areas. It was possible to select only two localities with assurance of their representing natural groups—Clingmans Dome and the Chimneys. In a sense they are fortunate choices as they represent the extreme known altitudinal limits for the species (6600 and 2800 feet, respectively). These two areas are the only

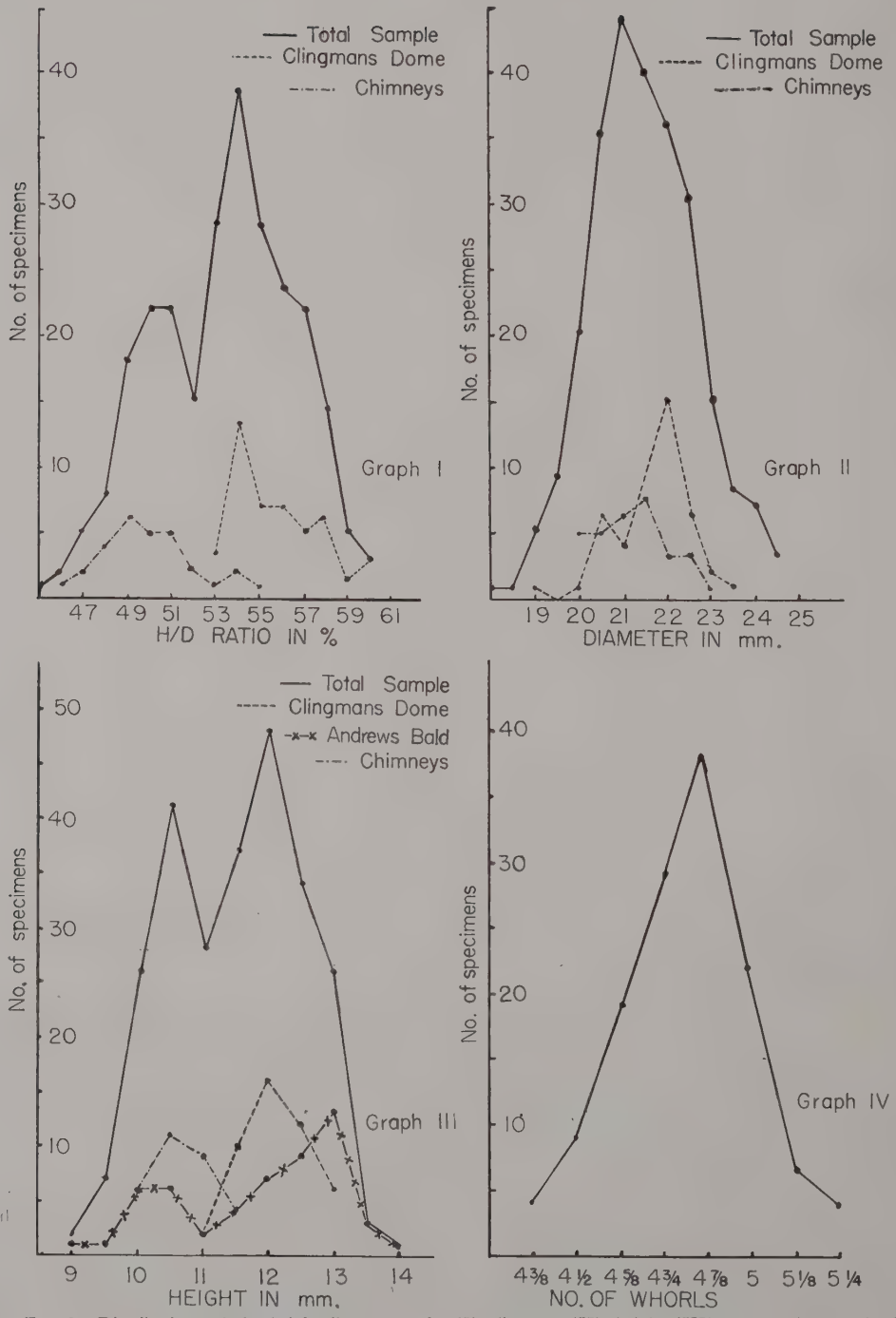

FIG. 2. Distributions of the height-diameter ratio (I), diameter (II), height (III), and number of whorls (IV) in a sample of 254 specimens of *Mesodon ferrissi*.

ones where it could be certain that the specimens would be representative of an actual breeding population rather than a series of populations. Many of the known lots were collected "on the trail from Mirey Ridge to Clingmans Dome" or "Mt. Leconte to Mt. Guyot" or "Mt. Collins to Clingmans Dome." Other areas with definite locality are unknown ecologically or represented by only a very few specimens. Enough specimens were found of the Sargent-Ferriss Andrews Bald collection to be treated, but they probably represent a biased sample as will be shown later. In order to assure the use of a single age group only fully adult specimens (those with a reflected lip) were used.

Results

The results of the statistical tests are given in Figure 2 and Table I. The graphs represent frequency distributions for the various parameters measured. The bimodality of the h/d ratio frequency curve (Graph I) is obvious. The sample of 254 specimens is large enough so that mere chance as a cause for the bimodality is unlikely. Charting the diameter (Graph II) and the whorl counts (Graph IV) produces a normal curve in both cases. Charting the height (Graph III) produces another bimodal curve indicating that height differences caused the bimodality in the h/d ratio curve.

It might be added here that a number of species were tested by Boycott (1928) for correlation between height and diameter with results varying from a correlation coefficient of 0.33 to 0.94. Similar tables for relating the height, diameter and whorl counts for *Mesodon ferrissi* produced correlation coefficients of 0.56 to 0.70, indicating there is no intrinsic close relationship between the three factors.

Table I. *Statistical summary of variation*

	No. Spec.	Mean	S. D.	Range
H/D Ratio				
All Specimens	255	53.3%	3.14	45.2-60.4%
Clingmans Dome	45	55.78%	1.94	53.5-60.4%
The Chimneys	29	50.0%	2.16	46.2-55.1%
Height				
All Specimens	254	11.47mm.	1.03	9.2-13.9mm.
Clingmans Dome	46	12.10mm.	0.527	11.0-12.9mm.
The Chimneys	30	10.69mm.	0.475	9.8-11.5mm.
Andrews Bald	55	11.82mm.	1.25	9.2-13.9mm.
Diameter				
All Specimens	254	21.46mm.	1.18	17.9-24.7mm.
Clingmans Dome	45	21.20mm.	0.95	19.2-23.7mm.
The Chimneys	30	21.18mm.	0.79	19.8-22.8mm.
Andrews Bald	55	22.07mm.	1.43	19.3-24.7mm.

The extremes of h/d ratio variation are shown in Figure 3. Both specimens were collected by the author in 1950.

Study of shells from the two geographic areas produced no difference in diameter, but a highly significant one with respect to height. Following Mayr, Linsley, and Usinger (1953: 146), the Clingmans Dome and Chimneys specimens could be placed in different subspecies (coefficient of difference is 1.41). It is certain that the specimens from the Chimneys represent a single population, but there is good evidence to indicate that the specimens on Clingmans Dome may have been drawn from two populations. Only two of the

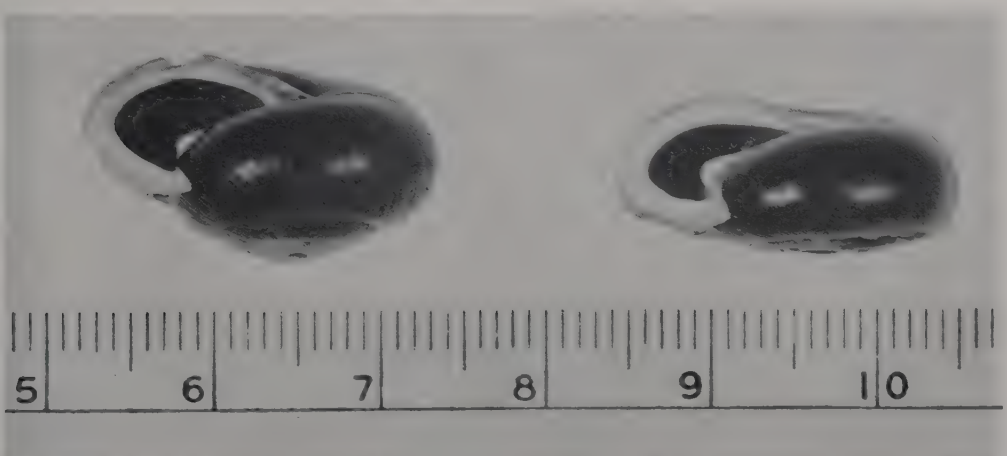

Fig. 3. *Mesodon ferrissi* Pilsbry. *Right*, high-spired specimen from Clingmans Dome; *left*, low-spired specimen from New Found Gap. The scale shows centimeters.

forty-six specimens from Clingmans Dome were less than 11.5 mm. in height. One of these, 11.0 mm. high, was collected by C. L. Hubbs "on the lower slopes of the mountain." The other specimen, 11.2 mm. high, is in the ANSP lot of the Ferriss, Sargent, Walker, Clapp and Pilsbry material. Pilsbry (1900: 121) stated, "Besides this locality near the summit of Clingman, a few specimens were taken from a similar station about one and a half miles down the west end of the mountain on the Tennessee side, probably near the 4000 foot contour." Since these specimens were not segregated from the other Clingmans Dome material, it is possible that the single small specimen is from this lower locality.

Specimens from Andrew's Bald present an entirely different situation. The range of height variation encompasses both ranges at the Chimneys and Clingmans Dome, yet presents a distinct bimodality. Since most shell collectors in making exchanges include large and small examples, and I have only observed about one-third of the Ferriss-Sargent material, it is probable that this bimodality is caused by bias in the sample rather than by any intrinsic ratio.

Discussion

Measurements of height and diameter indicate that there is significant intraspecific variation in the h/d ratio and analysis indicates that it is caused by variation in height of spire. On the basis of two selected localities, Chimneys and Clingmans Dome, it appears that the height variation is correlated with the ecologic difference of close-packed rock piles versus spaceous overhanging ledges. Low spire would be of definite advantage to forms in rock piles which under extreme conditions might have to retreat deep within the piles to escape desiccation, since this species is very sensitive to lack of moisture.

On the basis of two localities however, it is not possible to draw any definite conclusions. The specimens from Andrew's Bald present a difficult problem. Whether the area contains both rock piles and the ledges of Clingmans, with *Mesodon ferrissi* living in both areas, or whether factors other than the simple ecologic difference noted above control the height variation is a subject for future investigation.

Brown (1911: 161-4) discussed cases where differences in size and height of spire were correlated with altitudinal change. Previous workers had considered that the increase in height was caused by lower atmospheric pressure at greater altitude. Brown considered that the increase in spire elevation and over-all decrease in size from bottom to top of a hill was caused by interruption of moisture supply (*i.e.*, drying of ground cover) and consequent intermittent growth and stunting of the shell on the upper parts of the hill. The stunting caused a higher spire. While *Mesodon ferrissi* shows the elevated spire on the top of Clingmans Dome, there is no real difference in size between Clingmans Dome and the Chimneys, but only one in degree of elevation of spire. In addition, there appears to be no great difference in moisture supply between the Clingmans Dome and Chimneys habitats.

Conclusions

Study of 260 specimens of *Mesodon ferrissi* (Pilsbry) indicates a normal distribution of variation in diameter and whorl counts. Variation in height is seemingly correlated with ecologic factors, although this hypothesis needs testing and no information at all is available as to the nature of this variation, *i.e.* whether it is environmentally controlled or a genetically determined variant fixed by selection.

Summary

1. *Mesodon ferrissi* has been chosen for a long-range study of variation because of its size, restricted geographic and ecologic distribution, isolated taxonomic position, undisturbed habitat and cessation of growth at maturity marked by the formation of a reflected lip.

2. Historically this species has a relatively long record and geographically its range was found to be quite circumscribed.

3. The known ecology of *Mesodon ferrissi* seems to indicate special need for an unusually large amount of moisture.

4. The height and diameter of specimens in five museums and two private collections were measured to the nearest 0.1 mm. Whorl counts were made of 133 specimens. These figures were used in a simple statistical analysis.

5. Variation in both diameter and whorl count followed the expected normal distribution. However, the variation in height was bimodal and seemingly correlated with observed ecologic differences.

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THE CLASSIFICATION OF TROPICAL AMERICAN VEGETATION-TYPES

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In 1944, in a paper entitled "Climax Vegetation in Tropical America," the writer proposed a system of classification for the plant formations of the American tropics. In the decade since this paper was written, further experience has been acquired and our knowledge of this vegetation widened by the work of numbers of different authors. The writer has himself used the system in studies of the vegetation of Tobago (1944b), Trinidad (1946b), and the Windward and Leeward Islands (1949a). It has been put into use by Beebe and Crane (1947) in Venezuela, by Curtis (1947) in Haiti, and Wadsworth (1951) in Puerto Rico and, recently, (1952) has been followed by Fanshawe in his Preliminary Review of the Vegetation of British Guiana which constitutes its first application by another ecologist than its author on a large scale. Sundry interesting problems have been raised in the course of all this; definitions given and views expressed may require modification, and new plant formations can now be recognized. At this juncture, therefore, it is appropriate to make a review of the subject.

The broad principles of the original classification were laid down in the original paper and have been restated on two occasions (1945, 1949b). Briefly they are as follows. The basic unit is the plant association which is a floristic grouping, being the largest possible group with consistent dominants either of the same or closely allied species. Associations may be divided into minor floristic groups, to which it was proposed to apply the Clementsian terminology. Also, they may be termed consociations if they are single-dominant communities. Climax associations, that is, communities apparently mature, stable and integrated, may be further grouped together according to their structure and physiognomy into formations. The formation is a physiognomic group and is independent of flora. Communities which are situated in widely scattered parts of tropical America and for that reason are quite differently constituted may thus be classified into a single formation if of similar structure and physiognamy. The properties of the community express the habitat: the consistent dominance which defines the association expresses a constant local habitat within the regional flora and the consistent physiognomy which defines the formation expresses a constant essential habitat within the tropical zone. Types of habitat which are in general similar permit us further to group formations together into formation-series. There is thus a grouping at three levels: a floristic grouping—the association, a physiognomic grouping—the formation, and a habitat grouping—the formation-series. The association must bear a floristic name such as "*Eschweilera-Licania* association," the formation a physiognomic name such as "deciduous seasonal forest" and the formation-series a habitat name such as "montane formations." This rule may however be broken for formations in order to draw into the

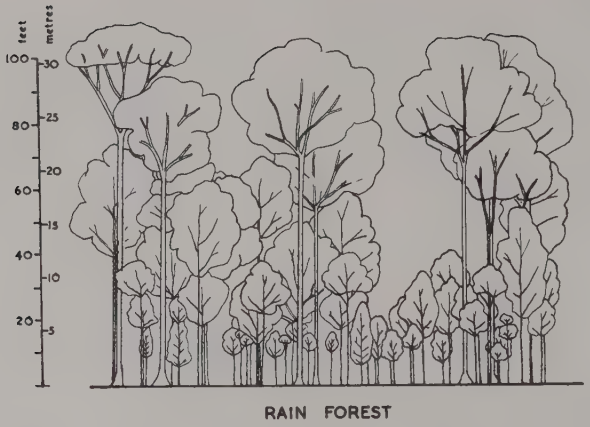

FIG. 1. "Type Specimen" of Rain Forest: the *Eschweilera-Licania* association of British Guiana, from the original diagram by Davis and Richards (1933).

classification well-established and understood names.

Twenty-six formations were described and defined in the original paper of 1944. One more, named "montane thicket" in English, was added to the Spanish translation published at Medellín in 1946. Another, "evergreen bushland," was defined in 1949 as a member of the dry evergreen formation-series. In the meantime also, it had appeared that one of the original formations, "palm-brake" might have to be dropped on the ground that it is a disturbance climax and not a natural climax of the same order as the other montane formations, work in the Lesser Antilles (Beard 1945b, 1949a) having led to this conclusion. To the twenty-seven climax types thus defined, Fanshawe (1952) has now added ten more, four in the dry evergreen, two in the seasonal-swamp and four in the swamp formation-series. A change of name in the seasonal-swamp series was also proposed. The discussion which follows below aims at consolidation of the classification to date.

An essential concept of the system is that rain forest (Fig. 1) stands alone, having both formation and formation-series rank, in the center, and that from it radiate the habitat groups in descending order from optimum to pessimum. The formation-series which has been best know hitherto is the seasonal group. A full series of five formations (six if "desert" is also illustrated) was defined and shown diagrammatically in the 1944 paper, repeated in 1946 and taken up by Richards (1952). This series is shown in Figure 2 herewith. It is envisaged that there is in reality one long unbroken series, in which the formations are artificially delimited stages. Each stage shows a regular stepping-down of structure. Rain forest has three tree stories, the uppermost one continuous. Evergreen seasonal forest also has three stories but the uppermost is discontinuous and canopy is formed by the second layer. In semi-evergreen seasonal forest only two stories remain, of which the upper is closed, and in deciduous seasonal forest this upper layer becomes discontinuous. Thorn woodland has only one tree story left, and in cactus scrub we have only the bushes and succulents. Desert retains nothing but a ground layer. Other physiognomic changes of course accompany the reductions of structure throughout.

We ought also to look for a similar regularly descending series of types in the other formation-series: not necessarily, perhaps, in the inundated swamp and seasonal-swamp series owing to their greater specialization, but certainly in the dry evergreen and montane series. In 1944, the writer did not have the data to substantiate this, and could illustrate the structure of only one dry evergreen formation and three montane ones. Now, however, more can be done.

Fanshawe (1952) has recognized six dry evergreen formations in British Guiana: Wallaba forest, xeromorphic rain forest, xeromorphic woodland, xeromorphic scrub, heath and littoral woodland. The choice of the name "Wallaba forest" was unfortunate, since wallaba is the vernacular name for the *Eperua* spp. which dominate the local association, and it is not desirable to give a floristic name to a formation. Supposing that forests of similar structure and physiognomy but not constituted by *Eperua* spp. are now described

FIG. 2. The Seasonal Formation-Series, after Beard (1944a) as redrawn in Richards (1952).

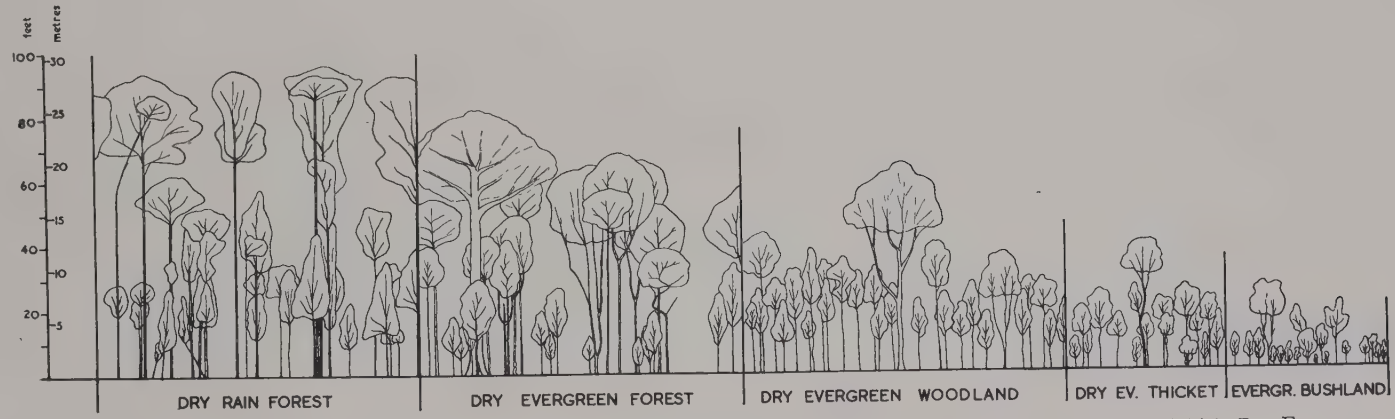

FIG. 3. The Dry Evergreen Formation-Series. Dry Rain Forest redrawn from Fanshawe's diagram of "Wallaba Forest" (1952), Dry Evergreen Forest from Beard's Xerophytic Rain Forest in 1944b, the remainder imaginary, from descriptions.

elsewhere, we cannot justifiably call them wallaba forests and some other term will have to be found. "Dry rain forest" is proposed as the most convenient term, since this formation lies very close to the true rain forest but is differentiated therefrom by the underlying white sands which are unretentive of moisture and cause a paradoxical dryness of the habitat. Xeromorphic rain forest is stated to be the same as Beard's xerophytic rain forest, with a minor change of terminology that has much to commend it, but the structure does not agree with Beard's definition. Xeromorphic woodland is a new formation. Xeromorphic scrub is the same as the evergreen bushland which had already been brought into the terminology (Beard 1949a). Fanshawe's use of "heath" here for an "herbaceous vegetation of "xerophytic lily-like plants" is surely inadmissible as there is no resemblance to the true heath of temperate climates. The writer suggests "rock pavement vegetation" as a substitute.

In attempting to consolidate the dry evergreen formations, the writer suggests first the elimination of the awkward terms "xerophytic" and "xeromorphic" in favor of "dry evergreen." We can next proceed to delimit our formations structurally with the aid of Figure 3. Nearest to the optimum comes the *Dry Rain Forest,* Fanshawe's "Wallaba forest," characterized as follows (adapted from Fanshawe):

> A three-storied forest with the canopy more or less closed between 25-35 meters, a discontinuous understory between 12-20 meters and a dense not very well-defined undergrowth from 6-12 meters. Illumination within the forest is relatively intense and the atmosphere dry. Stocking density is high and the trees are slender in relation to height. True under-growth species are few and the herb layers are poorly represented. Lianes are few and small. Epiphytes, especially sun epiphytes, are plentiful and descend low on the trees. Heavy buttressing is very rare. The proportion of semi-deciduous species is higher than in true rain forest. Leaves are mesophyllous, mostly compound in the canopy and simple in the understory.

Second in line of descent comes what we will now term *Dry Evergreen Forest,* equivalent to Beard's xerophytic rain forest but not to Fanshawe's xeromorphic rain forest. Reduction in structure now sees the canopy formed by a layer of crowded, slender trees reaching 12 to 20 meters in height above which an occasional emergent reaches 30 meters. Leaves are simple and evergreen, the majority being stiff and fleshy, a high proportion with latex or essential oil. Bark-shedding may be a conspicuous feature. The shrub and herb layers are poorly represented.

Thirdly, we have Fanshawe's xeormorphic rain forest, which we must now term *Dry Evergreen Woodland.* The understory of 6-12 meters is now the canopy-former, with emergents reaching 20 meters. Fanshawe describes this as:

> "A 2 storied forest with the canopy formed of densely packed, attenuated trees, now larger than 18-20 in. diameter (45-50 cm.) and about 20-40 ft. high (6-12 meters). There is a discontinuous emergent layer between 60-80 ft. high, made up of larger trees. The forest is almost entirely evergreen."

Fanshawe's xeromorphic woodland, which it is preferred to term *Dry Evergreen Thicket,* is to be considered as a valid new formation, characterized as follows:

> A 2 storied forest with a low, open, or dense canopy and a dense or sparse undergrowth. The canopy is between 20 and 40 ft. high (6-12 meters), and trees have slender stems not larger than 6-8 inches. (15-20 cms) diameter. There is an occasional, larger emergent.

Most reduced of all the woody formations is the *Evergreen Bushland,* Fanshawe's xeromorphic scrub, colloquially known as muri or moeri-moeri in the Guianas. This formation was detailed by Beard in 1949a.

Rock Pavement Vegetation takes the form of an irregular and open growth of herbaceous and woody plants less than two meters in height, growing in crevices or in mats of humus upon sheet rock, usually with much bare rock between. Such vegetation is frequently associated with outcrops of hard sandstone and granite bosses.

The 1944 formation *Littoral Woodland* must now be considered as identical with dry evergreen woodland, and the *Littoral Thicket* and *Littoral Hedge* (Beard 1949a) as dry evergreen thicket and bushland respectively. It may still be convenient to retain the names for particular studies, to differentiate dry evergreen vegetation under the influence of the sea, just as it is convenient to separate mangrove from freshwater swamp: but although the littoral habitat may be very different from that of inland sites carrying dry evergreen communities, we must recognize the essential physiognomic identity of these types. Differences such as the predominance of thickly cutinized salt-spray resistant leaves in littoral types must be regarded as of minor significance.

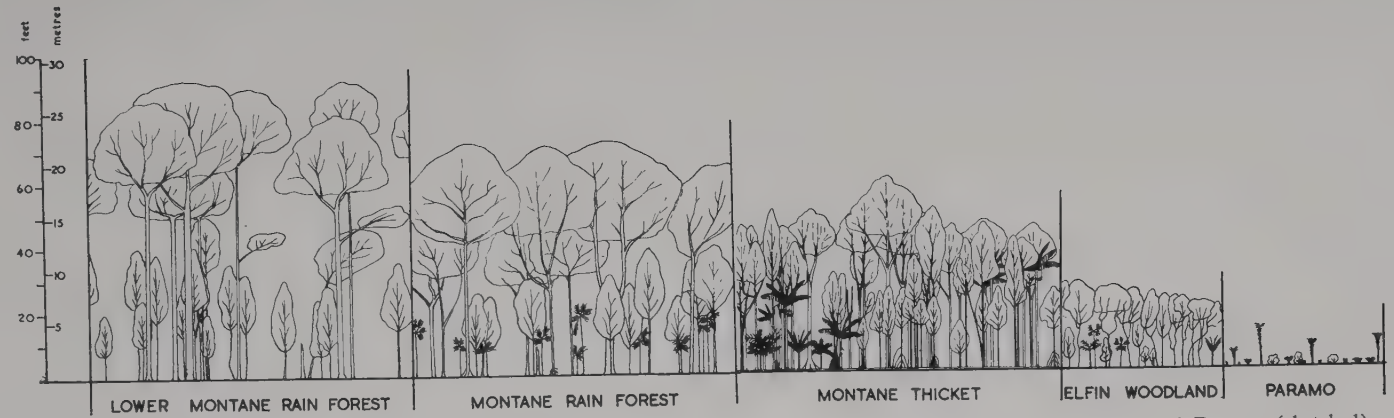

FIG. 4. The Montane Formation-Series, redrawn from Beard (1944a) with inclusion of Montane Thicket from 1949a and Paramo (sketched).

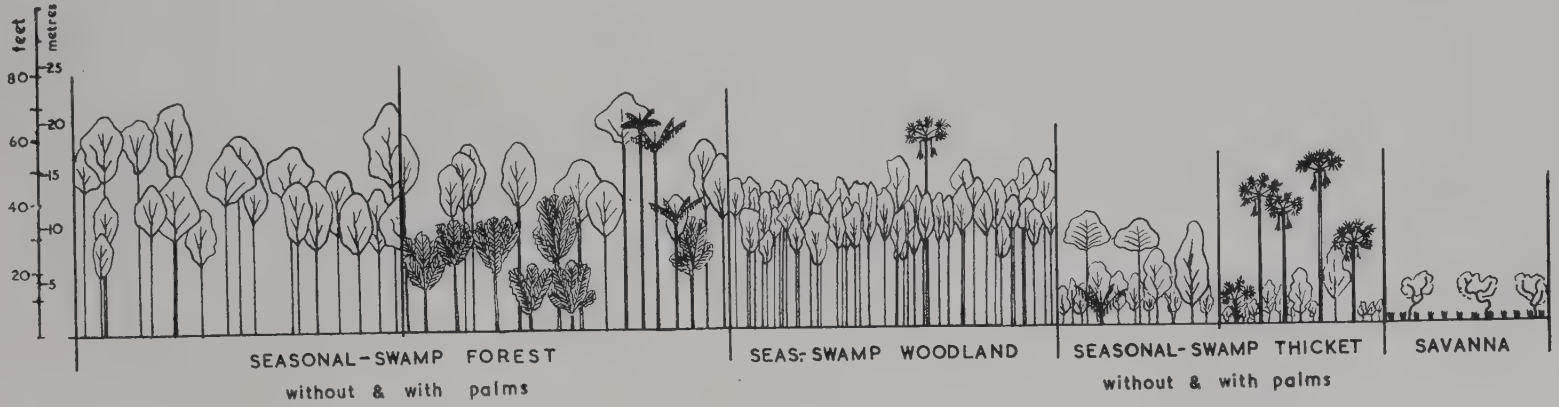

FIG. 6. The Seasonal-Swamp Formation-Series. Seasonal-Swamp Forests and Woodland redrawn from Fanshawe's diagrams (1952). Seasonal-Swamp Thickets after the Palm Marsh of Beard 1944a, Savanna diagrammatic.

It will be seen that the dry evergreen formations "step down" as their structure is reduced but not quite in the same way as the seasonal formations where successive strata become first discontinuous and then absent. In this way we seem always to have a canopy layer with emergent trees standing above it and little or no understory. As we descend the series, the height of these two layers is reduced.

We are now able to characterize the montane series of formations more fully than in 1944 (see Figure 4) and it will be seen that in this case the reduction of structure proceeds again somewhat differently. All forest-like montane formations present a continuous canopy layer without emergent trees and as we proceed through the series we find that the canopy layer is gradually lowered until finally it coalesces with the understory. On low mountains which do not rise above the upper limit of the mist belt (± 2,500 meters) the zonation is as shown in Figure 4. First and at lowest altitude, the *Lower Montane Rain Forest,* with two tree strata at 3-15 meters and 20-30 meters. Secondly, as the cloud belt is fully entered, comes the *Montaine Rain Forest* or *Cloud Forest* with the two strata reaching about 10 and 20 meters respectively (higher under favorable conditions). The above two formations featured in the 1944 account and there was an obvious discontinuity between the montaine rain forest and the elfin woodland, a gap which was filled in 1946a and 1949a by the inclusion of *Montane Thicket.* In this formation, the canopy layer is down to 10-15 meters and the understory is suppressed to the point of disappearance. Finally growth descends to the *Elfin Woodland* or *Mossy Forest,* a single-storied, impenetrable tangle, whose height varies from 10 meters down to one meter. Our terminology is not too good here, as we should correctly speak of montane woodland and elfin thicket; "elfin woodland" is however an old established name.

From studies undertaken (Beard 1945b, 1949a), it must appear that the palm brake (Fig. 5), although it may often appear stable, is a disturbance climax at an equivalent level to the montane thicket. In the Lesser Antilles, there can be no doubt that it is a successional stage on areas bared by wind, landslides, or volcanic eruptions. Wadsworth (1951) supports this view for Puerto Rico. Cuatrecasas (1934) has described a "palmetum" of *Ceroxylon andicola* in the Andes of Colombia occurring as a society in the "Clethrion" which appears to be montane thicket. No opinion is expressed as to its status. In view of the fact that the physiognomy of the palm brake is at variance with that of the other members of the montane series, it seems very probable that it never does constitute a true climax.

FIG. 5. Palm Brake, from Beard, 1949a.

On mountains rising to some extent above the mist belt, the elfin woodland gives place to the paramo. Closer acquaintance with this formation shows that it is in no sense comparable to an alpine meadow, as was suggested in 1944. It is much more similar to heath. The paramo finally gives way to the tundra at highest elevations. Where mountains rise so far above the mist belt as to carry a forest zone above it, we shall find a formation described as "frost woodland" in 1944 but which it is now preferred to call *High Mountain Forest. Mountain Pine Forest* is apparently a fire-climax derived from the latter and like the palm-brake must therefore be excluded from full rank in our classification. The writer has no structural data for high mountain forest. In zonation, it stands between cloud forest and elfin woodland. Further information on the *Bamboo Brake* proposed in 1944 indicates that *Chusquea* communities in the Andes are only of societal rank in the elfin woodland. There are *Guadua* societies also but these are riverain and at low altitude. It does not appear that we have any equivalent of the bamboo forest of East Africa and the Himalayas. The valid montane formations are thus reduced to seven.

The original four seasonal-swamp or "marsh" formations have been expanded to six by Fanshawe, who applies the name marsh to them. It is however highly debatable whether we should try to perpetuate the artificial distinction between "marsh" and "swamp" suggested by the present writer in 1944, in view of the fact that this distinction does not exist in common usage. While both represent inundated habitats, "swamp" is defined as having a perpetually waterlogged soil deprived of oxygen, whereas in "marsh" there is a fluctuating watertable permitting seasonal aeration of the topsoil. It seems generally preferable to substitute the term "seasonal-swamp" firmly for "marsh."

Four of his "marsh" formations are said by Fanshawe to occur in a regular zonation across the interfluves of the main rivers in the North-

west District, in this order: palm marsh forest → marsh forest → palm marsh woodland → palm marsh. The first named of these is at the river bank, which in a delta region stands higher than the ground level further away between the main channels. Away from these, seasonal rise and fall of the watertable gradually decreases and the vegetation is reduced. Actually, the true order of progression of the marsh series is not exactly in the order of this zonation, since the marsh forest is clearly the least reduced type of all and should stand at the head of the series. Evidently conditions are at the most favorable not in the palm marsh forest nearest to the creek but in the marsh forest belt slightly further away.

Our knowledge of the seasonal-swamp series has been greatly extended by Fanshawe but certain comments must be made. It does not now appear to the writer that the presence and absence of palms is such an important diagnostic feature as was previously suggested. There is little structural difference, apart from the palm question, between Fanshawe's marsh forest and palm marsh forest, nor between marsh woodland and palm marsh. As Fanshawe states that there are also palm-dominated variants of rain forest, seasonal forest and swamp communities in British Guiana, and there is a palm type of savanna as well, it seems that we should regard the seasonal-swamp communities with palms as merely variants also.

Figure 6 illustrates some of the variants but the main classification is consolidated to seasonal-swamp forest, woodland and thicket followed by savanna. There is in this case a considerable discrepancy between the head of the series and the optimum, within which no intermediates are known. The forest-like seasonal swamp formations are characterized by highly irregular canopy. It may be possible to define strata, but they are erratic and the forest canopy is now high, now low as growth varies from short to tall, dense to open. Passage through the series witnesses a progressive reduction in the stature of this jumbled assemblage.

Seasonal-Swamp Forest (without palms) is somewhat similar to dry evergreen forest and is defined by Fanshawe as follows for his "marsh forest":

> "A 2-3 storied forest in which palms only account for 5% of the stand. There is a low canopy of trees between 30-50 ft. (9-15 meters) and an emergent layer between 50-80 ft. (15-25 meters). Shrubs are more or less absent, but ground cover may be dense or sparse. Lianes are few, epiphytes fairly frequent. Buttresses are not marked. Leaves are evergreen, mesophyllous, 75% simple."

Seasonal-Swamp Forest with Palms is the original marsh forest of Beard. Palms here enter the assemblage in great numbers and become dominant, providing 40-60% of all trees and 60-75% of the lower story forms the canopy at 5-10 meters, and emergents, both trees and palms reach heights up to 25 meters.

Seasonal-Swamp Woodland is, after Fanshawe:

> "A low woodland of small-stemmed, regularly spaced trees with scattered emergent palms or trees of peculiar habit. The canopy lies between 30-50 ft. (9-15 meters) with emergent palms to 60 ft. (18 m.). The shrub layer is virtually absent; the ground cover sparse or dense. The mean tree diameter is 4 in. (10 cm.); emergents are from 16-36 in. (40-90 cm.) in diameter. The stocking is high—between 300-400 stems per acre, 4 in. diameter and over—but the flora is restricted to about 20 tree species. Lianes are few, epiphytes rare and these mostly hemi-epiphytes. Leaves are evergreen, mesophyllous, simple. Stilt roots are a common feature."

It is now clear that the *Amanoa* consociation described by Beard on the central plateau of Dominica (1949a) and tentatively classified as a "swamp phase of montane thicket" belongs to this formation.

The marsh woodland and palm marsh of both Beard and Fanshawe are now to be consolidated as seasonal-swamp thicket, without and with palms respectively. Savanna has been very fully dealt with by Beard in a recent paper (1953).

The original four swamp formations (swamp forest, palm swamp, herbaceous swamp, and mangrove woodland) have been expanded to nine by Fanshawe by the addition of four new formations and the recognition as full formations of the two former subdivisions of herbaceous swamp, now termed herbaceous swamp and semi-aquatic swamp. Not all of Fanshawe's treatment is, however, acceptable. At the pessimum he gives us aquatic swamp, "submerged trailing vegetation, attached to rocks in the shallow, fast running parts of the rivers." This would presumably include also the aquatic communities of lakes and ponds. All these are to be regarded as seral and unworthy of formation rank. We might very well, however, take up Fanshawe's term aquatic swamp for that division of herbaceous swamp which, at the true pessimum, consists of mats of grass rooted at the bottom but floating and rising up and down with

the water level. This was rather inaptly termed swamp savanna in 1944.

Between herbaceous swamp and swamp forest, Fanshawe has given us two useful new formations, *Arborescent Swamp* and *Swamp Woodland*. *Arborescent Swamp*, which for the sake of uniform terminology it is preferred to call *Swamp Thicket*, stands in shallower water, marks the appearance of woody growth and "consists of a dense growth of shrubby vegetation, on sand banks or stretches of silt, submerged at high tide or at high water. Woody species are restricted, but gregarious; shrubs, perennial herbs and lianes are occasionally associated" (Fanshawe).

Swamp Woodland is defined by Fanshawe as follows:

> "This term is proposed to connote the riparian fresh water fringe of low, spreading trees. Swamp woodland is remarkably homogeneous, comprises one or very few species and has a simple structure. There is one tree stratum 10-40 ft. high (3-12 meters) and the canopy is loose and open. A shrubby or herbaceous undergrowth may be present."

Swamp Forest and *Mangrove Forest* need no new definition are are the equivalents in fresh and brackish water respectively. They are to be regarded as fresh and brackish water phases of one and the same formation.

The above five formations constitute a harmonious series in reduction of structure. Neither of the remaining two types that we have to consider, Beard's palm swamp and Fanshawe's Mora forest, stands in a very satisfactory relation to the others and may have to be discarded. Palm swamp was not found by Fanshawe in British Guiana and in view of the probable modification by fire of the Trinidad swamps from which it was described, it is possible that it represents a fire climax, and is degradation of swamp forest or woodland, or of swampy normal forest. There may also be a confusion with seasonal-swamp types in some cases. Alternatively, as we have suggested that the presence of palms in seasonal-swamp types may not be diagnostic, "palm swamp" may be only swamp woodland or arborescent swamp in which palms happen to be present. Further data on this question are desirable.

Fanshawe's Mora forest is not a welcome member of this series. Apart from the nomenclature, which draws the same criticism as Wallaba forest, we cannot recognize it as a separate formation because the structure differs little if at all from rain forest and there is little or no other difference in physiognomy. The Mora may indeed be associated with wet riverain sites, but it should be regarded properly as a type of rain forest. It is true that the formation swamp forest is far removed from the optimum in structure so that we might expect to find other types to fill the gap. Mora does not fill any gap, however, because in structure it *is* optimum. This same hiatus occurs also as we have seen with seasonal-swamp types and is probably due to their specialization. There is less room here for intermediate stages, because the site is either inundated or not and the distinction tends to be clear cut. In the Trinidad forests, there are societies of species tolerant of wet ground, tending to resemble swamp forest, on low-lying sites but there is always an abrupt change to true swamp where permanent waterlogging occurs (see Beard 1946b: 67).

The classification of American tropical vegetation types is thus consolidated as follows. For reasons to be discussed, the montane series is now placed before the dry evergreen and we follow Fanshawe in taking seasonal-swamp before swamp. On balance, the consolidation has only added two formations to the previous total of twenty-six.

A. Optimum Formation.
   Rain Forest.
B. Seasonal Formations.
   1. Evergreen Seasonal Forest.
   2. Semi-Evergreen Seasonal Forest.
   3. Deciduous Seasonal Forest.
   4. Thorn Woodland.
   5. Cactus Scrub.
   6. Desert.
C. Montane Formations.
   1. Lower Montane Rain Forest.
   2. Montaine Rain Forest or Cloud Forest.
   3. Montane Thicket.
   3a. High Mountain Forest.
   4. Elfin Woodland or Mossy Forest.
   5. Paramo.
   6. Tundra.
D. Dry Evergreen Formations.
   1. Dry Rain Forest.
   2. Dry Evergreen Forest.
   3. Dry Evergreen Woodland and Littoral Woodland.
   4. Dry Evergreen Thicket and Littoral Thicket.
   5. Evergreen Bushland and Littoral Hedge.
   6. Rock Pavement Vegetation.
E. Seasonal-Swamp Formations.
   1. Seasonal-Swamp Forest.
   2. Seasonal-Swamp Woodland.
   3. Seasonal-Swamp Thicket.
   4. Savanna.

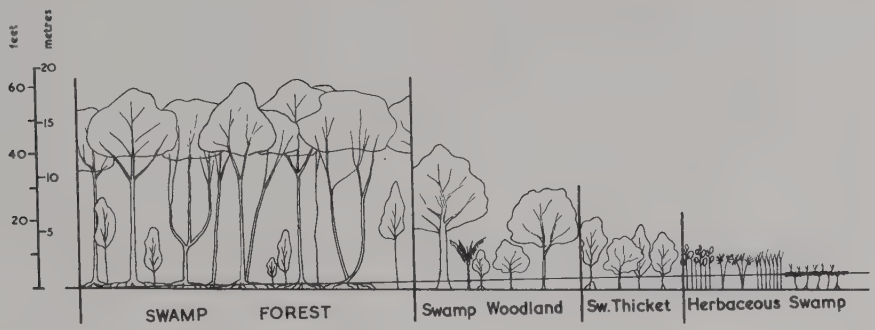

FIG. 7. The Swamp Formation-Series. Swamp Forest after Beard, 1944a, the remainder imaginary and diagrammatic.

F. Swamp Formations.
1. Swamp Forest and Mangrove Forest.
2. Swamp Woodland.
3. Swamp Thicket.
4. Herbaceous Swamp.

Space does not permit a recapitulation here of the physiognomic details of these formations and it is assumed that students of the question will be familiar with the earlier papers cited. The twenty-eight formations characterized should now be adequate to include all the possible types of vegetation in tropical America apart from "atypical formations" as envisaged in 1944a. Caution must be exercised in attempting to apply the system. It will not fit secondary or damaged forests, seral communities nor local societies, some of which, like the riverain *Guadua* bamboo groves of Colombia, may differ strongly from the climax association.

Certain observations on the habitat of the formations will now be made, since some of the original conceptions have to be modified. Fanshawe's work emphasizes in strong measure the overwhelming importance of soil drainage in controlling the vegetation of high rainfall areas. In dry and moderately dry areas, the most important character of the soil is its moisture-supplying ability, in which the drainage factor assumes a smaller and smaller role as the dryness of the climate increases. In wet areas, however, as the wetness increases only sites of increasingly favorable relief and physical structure of the soil are able to dispose of surplus water by run-off or infiltration and continue to support unspecialized vegetation. Even here, paradoxically, we can also find soils whose drainage is at the other extreme and too free. The climatic climax, in its narrow sense, can only exist on sites where drainage is optimum and neither too free nor impeded. In British Guiana, climate differentiates the rain forest from the seasonal forests of the eastern border and from the montane forests of higher altitudes in the Pakaraimas. It is drainage which separates from these the enormous areas of dry evergreen, seasonal-swamp and swamp.

There is nothing to be added at this stage to our knowledge of rain forest and seasonal forests. These can only occur on well-drained sites and are invariably predominantly controlled by climate. Locally, sites of poor moisture supplying ability will carry vegetation of a drier type than the regional climax, and unusually favorable sites vegetation of a more luxuriant type. In such cases seasonal formations are still present and show only a move up or down in the formation-series.

Montane formations likewise reflect essentially the climatic zonation associated with altitude and have for this reason been placed next in the classification, rather than the dry evergreen formations which are less clearly climate-controlled. Generally speaking, rainfall and humidity increase progressively up to a level of some 2,500 meters, above which there is again a progressive decrease. Temperature falls steadily with altitude, but only becomes critical above about 3,000 meters. At this level and upward it must be responsible for the zonation of high mountain forest, elfin, woodland, paramo, and tundra below the snow line at about 4,500 meters. In different regions rainfalls vary widely within this zone without changing the essential character of the vegetation. There are both wet and dry paramos. Lower down in the cloud belt exposure becomes a factor of great importance and is responsible for alternations of lower montane and montane rain forest with montane thicket and elfin woodland. The more reduced formations are found to come in on ridge tops, very steep slopes or areas particularly exposed to the prevailing wind. Below 2,500 meters, the vegetation is still essentially tropical and it seems unlikely that temperature has any effect on

zonation which is primarily due to the exposure factor. In previous papers the writer suggested that the exposure could result in excessive transpiration on clear days and that this was largely responsible for the reduction in stature and leaf size. It now seeems that this view is not tenable. "Exposure" is compounded of numerous effects. Most important of these is probably the mechanical effect of wind, which could break or blow down large trees on exposed ridges and slopes with shallow soil. The exposed situations in the mist belt are those where fog forms most consistently and where humidity and precipitation are highest. This may reduce transpiration to the point of stunting growth of the trees. A further limitation will be imposed by lack of root-room on steep slopes: however high the rainfall, shallow soil is bound to mean a lower forest. Again, in certain cases, the perpetual wetness of the climate sets up impeded drainage conditions even on mountain slopes, accentuated by pan-formation and the accumulation of a saturated surface peaty layer, with resultant reduction of the vegetation. This was found to be the cause differentiating montane thicket from lower montane rain forest in Puerto Rico by Wadsworth and Bonnet (1951). In such a case the montane thicket becomes close to marsh woodland.

Of the remaining three formation series, seasonal-swamp and swamp are clearly edaphic formations while the dry evergreen occupy a somewhat intermediate position and may be termed edapho-climatic. The swamp types are the most specialized, growing in permanently or more or less permanently inundated ground. The seasonal-swamp formations are in a sense intermediate between true swamp and dry evergreen, being periodically inundated on the one hand and associated with soils of obstructed internal drainage on the other, while the dry evergreen formations stand between seasonal-swamp and the truly climatic seasonal and montane types. These affinities between the habitat groups are shown by the certain degree of floristic interchange which takes place in a horizontal direction between them. Certain trees such as *Symphonia globulifera* are at home in both seasonal-swamp and swamp, while *Clusia fockeana* may be a dominant in both seasonal-swamp woodland and dry evergreen woodland in British Guiana.

Seasonal-swamp and swamp formations are in a true sense edaphic. Entirely under the influence of ground water, they will appear in substantially the same form under any climate where the edaphic conditions are similar. They stand moreover in a clear developmental relationship to the climatic climax, occupying sites which are capable of evolving towards an optimum or have already devolved away from it. The dry evergreen formations are more difficult. Where littoral types are concerned they are controlled by climate, but it is a local and not the regional climate Dry evergreen forest which seems formerly to have existed in the Lesser Antilles at low altitude (Beard 1949a) would have been controlled by climate and climate induced soil conditions in "terras" and "shoal" soils which had developed drainage impedance. Dry evergreen formations in the interior of British Guiana are all differentiated from the climatic optimum by soil conditions, but these vary widely: In the white sands, we have a peculiar soil type of excessive drainage, which is not a climate-induced development, nor will it be capable of developing in any direction except by topographic senilty: there is no developmental relationship, therefore, between dry rain forest and the climatic climax. On the Kaieteurean sandstones, the dry evergreen vegetation occupies immature soils, where the rock has not yet decayed deeply: as it does so, there is presumably a development towards the climatic climax. Yet again, we find dry evergreen on ridges of lateritic ironstone, senile soils that have developed gradually the lateritic horizon: as they did so, there was presumably a development away from the climatic climax. Unlike seasonal-swamp and swamp formations, dry evergreen are always to some extent controlled by climate. Seasonal-swamp and swamp will be the same under any climate if groundwater conditions are constant whereas dry evergreen vegetation on a given soil type will vary according to the prevailing climate. The ecological status of dry evergreen formations may frequently appear to vary widely, but they are united by their essential habitat. An essential similarity of moisture relationships accounts for the fact that the same formation may appear on such widely different soil types, now deep white sands, now shallow sandstone, and now rocky laterite ridges.

There is little difficulty in assessing the habitat of swamp formations which are in general differentiated by the depth and duration of inundation, with salinity and aeration of the water and nature of the rooting medium as subsidiary factors. Seasonal-swamp vegetation is always associated with impeded drainage of the type which will lead to stagnation of the ground water and deprivation of oxygen, occurring on flat areas having a pan or impermeable subsoil or simply a high water table and deficient means of lateral drainage. In true swamps, water-logging is always present and

the ground can never dry out. In seasonal-swamp there is at least a fall in the water table, allowing seasonal aeration of the topsoil. It is this factor which appears to control the segregation of these two major groups of edaphic communities. Under a strongly seasonal climate, waterlogging and stagnation of ground water take place on ill-drained sites during the rainy season while in the dry due to the nature of the soil there comes a period of desiccation. This acute alternation of moisture conditions is too severe for tree growth and is the commonest cause of the appearance of savanna. In higher rainfall areas, such severe seasonal desiccation may never occur, but there will be a relatively dry period of more favorable conditions in sites of bad drainage and stagnant ground water, giving us the woody seasonal-swamp formations, which are differentiated by the drainage factor into the series of formations, seasonal-swamp forest occurring where the drainage conditions are least severe and at the other extreme seasonal-swamp thicket standing for long periods in relatively deep stagnant water.

It is drainage variations which determine the zonation in and around savannas. With rainfalls of upwards of 2000 mm. a year, sedge savannas are most often found and occur typically as relatively small patches surrounded by a zonation of seasonal-swamp types from thicket to forest, these woody formations being enabled to appear due to the preponderance of the waterlogging factor. With rainfalls between 1000 and 2000 mm. a year, conditions on flats with impeded drainage are ideal for savanna, there being sufficient seasonal periodicity in the rainfall to maintain an intense alternation of the water conditions. This is the niche of tall bunch grass savanna which occupies wide areas, including sites which under higher rainfall would be constantly wet and carry woody seasonal-swamp vegetation. The transition to adjoining climatic forest is now usually abrupt, without ecotones or intermediate communities. An intermediate stage can however, sometimes be found where the rainfall is about 1500 mm. or less and the savanna is surrounded by semi-evergreen or deciduous seasonal forest. In such a case there may be a belt, called *cerradão* on the Brazilian plateau (Waibel 1948) and which we may perhaps term savanna woodland, constituted by a closing-up of the savanna trees to form a dense woodland 10-15 meters high. As the flora is still essentially that of the savanna, this must be considered as properly a type of savanna rather than as a separate formation. Under rainfalls below 1000 mm. a year, the waterlogging factor begins to fade out and is only now severe in depressions. The low rainfall accentuates relief, so that the climatic climax—thorn woodland and cactus scrub—comes in on all the slight rises to form an intricate mosaic with short-bunch grass savanna which occurs as small patches in the slight depressions.

Dry evergreen communities not infrequently associate with savannas, appearing on reefs of white sand where rooting depth becomes very great, or on rock outcrops where rooting depth is greatly reduced: drainage is however good in both cases.

Summary

The classification of plant formations in tropical America proposed by the writer in 1944 is reviewed in the light of subsequent work, particularly of Fanshawe's "Vegetation of British Guiana" (1952). The original twenty-six formations are expanded to twenty-eight, listed in the text on p. 96. The physiognomy and habitat of these formations are discussed.

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THE RELATIONSHIP OF WATER ECONOMY TO TERRESTRIALISM IN AMPHIBIANS[1]

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INTRODUCTION

One of the most essential requirements for life on land is the ability to avoid excessive loss of water from the body tissues. Among the terrestrial vertebrates, reptiles, birds, and mammals have met this requirement more or less effectively by the acquisition of an impermeable integument or integumentary modifications such as scales, feathers, and hair, and by the ability to excrete waste products not accompanied by large quantities of water. Amphibians, on the other hand, have no extensively developed integumentary modifications that tend to conserve body water. Even in the most terrestrial species, the integument itself offers little resistance to water loss, but on the contrary, loses water freely by evaporation. Furthermore, as far as is known, amphibians always excrete hypotonic urine. Perhaps largely because of their failure to meet the requirement of water conservation effectively, amphibians are in general confined to water, the vicinity of water, or at least to moist places or moist soil. As a terrestrial vertebrate group, they have not been markedly successful.

Despite the apparent lack of a highly effective water-conserving mechanism in amphibians as a group, marked differences exist between species in their degree of dependence on water. Some species are restricted to water throughout life, a few have been completely emancipated from open water even in their embryogeny, while the remaining species are distributed between the two extremes.

Because of their diversity as regards independence of water, and since they are a group showing transition from the aquatic to the terrestrial environment both historically and developmentally, amphibians are peculiarly appropriate subjects for investigations concerning the role of water economy in the development of terrestrialism.

In the amphibian body there are several sites of water exchange where water may be introduced into the system or lost to the environment, and on which water-conserving mechanisms could therefore conceivably act: (1) Throughout the body, wherever oxidation takes place, metabolic water is produced. This is added directly to the watery medium of the protoplasm and is subject to loss from the body only indirectly as any excess water of whatever source is subject to elimination. In any case, the production of metabolic water in amphibians amounts to less than 0.01% of the body weight per 24 hrs. at 20° C (Adolph 1943) and thus scarcely needs be considered. (2) In mammals, birds, and other animals that take water into the body by mouth, the absorption of ingested water into the system through the lining of the digestive tract is an extremely important consideration in any study of water metabolism. However, among amphibians, although about one half of the total water uptake of tadpoles is by mouth (Rey 1937), adults do not drink except under certain abnormal conditions as following dehydration due to immersion in salt solutions of relatively high concentration (Overton 1904). Thus the alimentary canal is not an important site of water exchange except in the degree to which water is ingested as a component of the food and egested with fecal matter. Since the animals used in the following experiments were kept in a fasting condition, intestinal exchange of water has not been a problem. (3) In air-breathing forms, the lungs dissipate a small and probably fairly constant quantity of water into the atmosphere. In the saturated or nearly saturated atmosphere above the surface of a body of water or in other moist surroundings fre-

[1] This investigation was conducted largely in the Department of Zoology of the University of Washington. It was supported in part by the University Research Council and the Department of Zoology of the University of Nebraska.

quented by most amphibians, this loss would be practically nil. In a dry environment over a long period of time, the loss could be of considerable proportions. However, during the comparatively brief time covered by most of the following experiments, loss of water via exhalation would presumably be negligible, and so has been disregarded. (4) Particularly while in the water, the amphibians' kidneys are continually excreting comparatively large quantities of dilute urine. In a water medium, practically all the water lost escapes by way of the kidneys. When removed from water, amphibians cease producing urine at once (Adolph 1927), or after losing a certain percentage of the body water by evaporation (Rey 1937). Under the conditions of the present experiments, the quantity of urine produced must necessarily be very small or nil, and while losing water by evaporation, amphibians were never observed to expel urine. (5) In an environment of air, particularly under conditions of desiccation, water is lost almost exclusively through the skin by evaporation, while in a water medium there is a continual net uptake of water through the skin. Out of water, there can be no uptake of moisture through the skin even in saturated air. When no evaporation occurs the body temperature of the frog is slightly higher than the ambient temperature, thus bringing about a slight loss through evaporation rather than an uptake (Adolph 1932).

In species of amphibians that alternate between periods of time spent in water and out of water, the characteristics of the water economy necessarily differ sharply in the two media. Most of the studies made to date have concerned the nature of the water economy of animals *in water*. A host of contributions to this subject has been reviewed by Adolph (1933, 1943), Krogh (1939), Prosser *et al.* (1950), and by Rey (1937) in an important paper overlooked by most American investigators. These investigations have contributed greatly to an understanding of amphibian physiology. However, they are studies of amphibians as *aquatic* animals. A more direct approach to the problem of the amphibian invasion of a terrestrial environment would seem to be the study of amphibians as *terrestrial* animals, by an examination of water exchanges as they occur in the air, since the atmosphere is the critical medium in making this ecological transition.

Although the general features of water metabolism are similar in different species of amphibians, the fact that considerable ecological diversity exists in the group suggests that quantitative differences must exist in certain physiological characteristics of the water economy. These, if discovered and found to be correlated with the degree of independence of water, might yield clues as to factors which have made possible the development of terrestrialism among amphibians.

The present study is therefore an attempt to disclose features of the amphibian water economy, comparing species when possible, which may throw some light on the problem of the development of terrestrialism in this class of vertebrates. The approach is from the standpoint of amphibians as terrestrial animals which have been studied largely through measurements of water lost through the skin by induced evaporation, or uptake of water following such desiccation.

The general problem has been approached from several angles, each of which can best be discussed individually.

Materials and Procedures

Most of the experiments reported in this paper were performed with the use of one of two types of desiccator.

The simpler type consisted of a glass jar approximately twelve inches tall and five inches in diameter, of 3.6 l. capacity and equipped with a loosely fitting lid. A glass dish containing anhydrous calcium chloride as a desiccant was suspended just below the lid. Another dish of calcium chloride fitting into the bottom of the jar was covered with a piece of wire screen which formed a platform on which the specimen rested during desiccation. The desiccant was changed regularly to assure a strong water-absorbing action.

The second type of desiccating apparatus employed the same kind of jar but instead of using calcium chloride, air was forced through the chamber from the compressed air supply in the laboratory after passing through a system designed to remove the moisture and regulate the rate of flow. The moisture from the air was removed by bubbling through a series of three large bottles of concentrated sulfuric acid followed by a bottle containing sodium hydroxide pellets to neutralize any acid fumes and a layer of powdered charcoal between two layers of glass wool. The air passed through another small bottle of glass wool immediately before entering the desiccating chamber. Air flow was maintained at a constant rate in spite of fluctuations in the pressure from the source by means of a mercury column pressure release. The air before flowing through the first sulfuric acid bottle had access to an alternate path when the pressure arose high enough to force the air down through a glass tube with its end submerged in a large test tube of mercury. The

height of the column of mercury was adjusted to allow the air in excess of that desired to escape. The air flow in each of eight systems was checked periodically by means of a "Precision" wet test meter and adjustments were made as necessary to keep the flow at 2 l. per minute.

Most of the experimental work was done on *Rana pipiens* procured from Wisconsin supply houses throughout the year. For certain comparative work, *Scaphiopus hammondii,* collected during the month of May from breeding ponds near Vantage, Washington, and *Rana clamitans,* obtained from Wisconsin during May, were also used. For one series of experiments, *Rana catesbeiana* from a California firm, and *Bufo boreas* collected near Duvall, Washington, both obtained in April, were used in addition to the three species above.

Before use, the animals were kept at room temperature without feeding, in a 2 x 8-foot stainless steel tank through which a slow stream of tap water was passed continuously. Amphibians to be desiccated were dried with paper toweling, weighed in a plastic dish, and placed singly in desiccators. After the desired length of time they were removed, weighed again, allowed to regain the body water lost during the experiment, and whatever computations desired were made.

Most of the experiments were performed in a room whose temperature was maintained thermostatically at 24° C with a fluctuation of not more than two degrees plus or minus.

Certain variations in procedure and experimental conditions will be noted as they occur and further details will be presented as necessary.

Resistance to Water Loss

The ability of successful land vertebrates to live out of water is due in a large measure to the presence of an integument which prevents undue loss of body water through evaporation. In this respect amphibians are poorly adapated to life on land. As an illustration, the water loss of an amphibian, *Rana pipiens,* was compared to that of the garter snake, *Thamnophis sirtalis,* the latter a species well adapted to terrestrial life by virtue of its scale-covered skin. Both were desiccated under the same conditions in an air flow desiccator described above. The snake weighing 16.7 grams lost 13.1% of its body weight in seven days, whereas frogs of comparable weight lost an equal proportion of water in but two to four hours, a rate more than 40 times that of the snake. Hall (1922) has shown that a lizard (*Sceloporus spinosus*) weighing 38.3 grams and a horned lizard (*Phrynosoma cornutum*) of 31.5 grams under fairly comparable experimental conditions lost about 13% of their body weight in approximately 38 and 45 days respectively. The water-conserving action of the integument of reptiles appears even more striking when one considers that during these long periods of time, much of the water loss must have occurred by way of expired air rather than through the skin. Rey (1937) stated that evaporation from the skin of amphibians took place at about the same rate as evaporation from open water or perhaps even more rapidly because of the many tiny tubercles in the skin which increase the evaporating surface. Thus the amphibian skin affords no protection from drying.

Ineffective as amphibian skin in general may be in resisting water loss, there are, as will become evident later, certain differences in rate of water loss between species. If such differences between species could be shown to be correlated with the degree of terrestrialism, a good case could be built for resistance to desiccation as a factor in determining amphibian habitats. Such a correlation seems to be taken for granted in popular literature and even in more technical works, for statements are made to the effect that toads can live in drier places than frogs because the former have a drier or thicker skin and thus lose water less readily. However, investigators who have applied experimental procedures to the problem are by no means unanimous in their agreement with this assumption.

Scala (1936) claimed to have demonstrated a correlation between the rate of water loss and habitat preference, showing that Bufo lost water appreciably more slowly than Rana, and Rana in turn at a slower rate than Triton. Bufo was regarded as terrestrial, Triton as the most aquatic, and Rana as intermediate. Unfortunately, Scala did not give sufficient attention to the almost universal observation of investigators of amphibians in air that small animals lose water more rapidly than large ones. This phenomenon is due to the well-known fact that small bodies have a greater relative surface area than larger ones. The bufonids used by Scala averaged nearly 50 grams in weight, more than twice the size of the ranids and more than five times as large as the tritons. Corrections for size would tend to reduce the differences in the rate of water loss shown by Scala's paper. The degree of difference between species in resistance to loss of water was great enough so that the use of animals of comparable size might still have resulted in the same conclusions. Nevertheless, the failure to consider size detracts from the conclusiveness of the data. The results of Cohen (1952) tend to support those of Scala.

When the rates of evaporation from two plethodontid salamanders were compared, the water loss of *Ensatina eschscholtzii xanthoptica* was more rapid than that of *Aneides l. lugubris.* The latter in its natural environment tends to be somewhat less dependent on moisture than the former. Although Aneides showed approximately the same rate of water loss as the somewhat less terrestrial *Triturus torosus,* the mean sizes of experimental animals were not comparable. Considering only comparably sized individuals of these two species, Triturus lost water appreciably more rapidly, despite a heavier integument. Rey (1937) compared animals of approximately equal size and showed that four species inhabiting diverse habitats, *Rana esculenta, R. temporaria, Triton marmoratus,* and *Salamandra maculosa,* all lost water at very nearly the same rate, approximately three milligrams per hour per square centimeter of body surface. However, the toad, *Bufo bufo,* lost at a somewhat slower rate (ca. 2.5 milligrams per hour per square centimeter of body surface). Adolph (1930) stated that toads (apparently *Bufo americanus*) evaporated just as rapidly through the skin as frogs (probably *Rana pipiens*). He did not quote specific data in support of this statement, nor did he describe his method. Kirk and Hogben (1946) reported that toads did not give up water more slowly than frogs. They based their claim on the fact that under the same experimental conditions, *Bufo bufo* and *Rana temporaria* of approximately equal size underwent very nearly the same depression of body temperature due to evaporation. Overton (1904) stated that *Rana temporaria,* in spite of its thinner skin, lost water somewhat more slowly than *R. esculenta* of the same size and under the same conditions.

It is evident that the results of experimental investigations concerning the resistance of the skin to water loss as a factor in amphibian ecology are inconclusive and even contradictory. Whereas it appears to be true that no strikingly resistant skin has been developed in this group, the work referred to above, as well as preliminary investigation by the writer, indicate that there is some variation among species in this respect. Since the lack of agreement may have resulted from the use of different experimental procedures, comparison of anurans with urodeles, and perhaps by failure in certain cases to take size into consideration, a re-examination of the whole question appeared to be in order.

Five species of amphibians, all anurans, have been studied. *Rana clamitans* and *R. catesbeiana* are among the most aquatic of North American anurans, *R. pipiens* being considered as semi-aquatic, whereas *Bufo boreas* and *Scaphiopus hammondii* are both almost independent of open water during most of the year. Of the latter two species, *Scaphiopus hammondii* is a fossorial form, burrowing in moist soil and occurring in the more arid parts of the West, while *Bufo boreas* lives above ground and thus must cope with more rigorous conditions of water loss than Scaphiopus.

In order to compare the species to the best advantage, as wide a range of sizes as possible was used in each case. Scaphiopus was comparable only with the small individuals of the other species since its size range is restricted, and only small to medium-sized *Rana catesbeiana* were used, for none of the other adult species compare in size with large bullfrogs.

Each animal was desiccated for a period of 10 hours. The air-flow desiccators described above were used with the standard rate of 2 l. air flow per minute at room temperature. The percentage of body weight lost during 10 hours was computed and this has been plotted against size for each species in Figure 1. Forty-two *Scaphiopus hammondii* were used, 55 *Rana clamitans,* 56 *R. catesbeiana,* 85 *R. pipiens,* and 20 *Bufo boreas.*

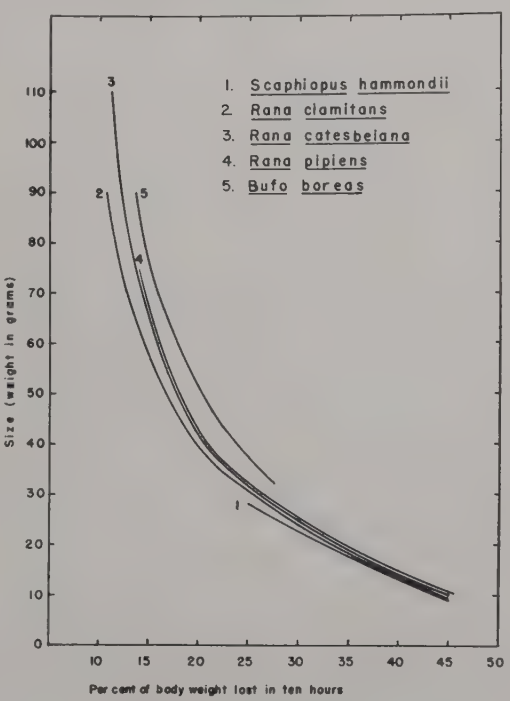

FIG. 1. Resistance to water loss. The difference in the rate of water loss between 5 species indicates the relative effectiveness of the skin in retarding desiccation. The effect of size on the rate of water loss is also demonstrated.

The influence of size on the rate of water loss within each species is immediately apparent from Figure 1. The large animals with less surface per unit of bulk lost water proportionately more slowly than small animals in which the ratio of surface to volume is high. In *Rana catesbeiana* for instance, in which the size range was greatest, the largest frogs lost only about one fourth as great a percentage of their body weight as the smallest animals in an equal length of time. The other species demonstrated almost identical relationships of size to rate of dehydration within the limits of their size range.

Figure 1 also indicates that among the smallest animals, only slight differences exist between species in resistance to loss of body water through evaporation. In the larger sizes, on the other hand, the divergence in rate of water loss increases, and pronounced differences are apparent. However, the differences are not correlated with habitats as reported by Scala, but are, on the contrary, almost exactly reversed in order. *Rana clamitans,* an aquatic species, lost water at the slowest rate, while *Bufo boreas,* a terrestrial species, lost water most rapidly. Between the two extremes were the aquatic *Rana catesbeiana* and the semi-aquatic *R. pipiens* exhibiting almost identical curves. Of the five species, only *Scaphiopus hammondii* showed a relative rate of water loss which might have been expected from its habitat. It lost water more slowly than any species of comparable size, although the difference is not great. In this size range, however, the other species occur in the same order as they did in the larger size range.

It can be stated therefore that, in the species studied, no correlation exists between the resistance of the skin to water loss and the degree of independence of water. These data fail to support the hypothesis that the development of resistance to desiccation has been an important factor in the appearance of terrestrialism among amphibians.

There appears also to be no correlation between the smoothness or roughness of the skin and rate of water loss. Noble's (1931) statement that smooth, thin skins are more subject to desiccation than thicker, more cornified ones, is not supported by the data in Figure 1. *Bufo boreas* has a thicker, rougher, and drier-appearing skin than any of the other four species, yet it loses water more rapidly than any of them. Very likely the tubercular nature of the skin of this species, by increasing the effective evaporating surface, results in the more rapid loss of water.

Uptake of Water Following Desiccation

A second characteristic of the amphibian water economy which might be of survival value to these animals in a terrestrial habitat is the ability to absorb water quickly. Other things being equal, a species capable of absorbing water readily from its environment following its loss through evaporation would have a greater potential for survival on land than a species in which uptake took place less readily. Such an ability seems especially significant when one considers species that remain away from water for long periods of time. All amphibians are subject to rapid water loss through evaporation, so it appears essential that a terrestrial species be able to absorb water readily when the opportunity presents itself in the form of rain, dew, moist soil, etc. It has been demonstrated (Adolph 1932) that amphibians cannot absorb water from the air even though it be saturated. This was confirmed by the writer, using *Scaphiopus hammondii.* After desiccation to a loss of 35.4% of its original 13.3 grams, a toad continued to lose water slowly for two days even though placed directly above open water in a closed jar.

The rate of uptake of water through the skin of normally hydrated amphibians in water can be determined by canulation of the cloaca and measurement of urine production, or by ligation of the cloaca and observation of the increase in weight. This has been done by numerous investigators. Rey (1937) compared the rates of uptake in hydrated animals of five species and found that the terrestrial species absorbed water more rapidly than aquatic types. *Bufo vulgaris* and *Salamandra maculosa,* terrestrial toads and salamanders respectively, absorbed water at rates four or five times those of the more aquatic *Triton marmoratus* and *Rana esculenta.* Jørgensen (1950) obtained essentially the same results using *Bufo bufo* and *Rana temporaria,* although dissimilar experimental conditions resulted in somewhat different absolute values.

These studies made by Rey and Jørgensen were concerned with amphibians *in water,* and therefore functioning as aquatic animals. Although their findings may have a direct relationship with uptake by amphibians out of water, a demonstration of the rate of water uptake as an aid to amphibians on land requires a comparative study of the rates of uptake in dehydrated animals, since it is only under conditions of water deficit that a high rate of uptake would be an asset.

Concerning the loss of water from amphibians by evaporation, most investigators have noted the

great rapidity with which rehydration takes place after the animals are replaced in water. However, literature concerning the comparison of species in this respect is very meager. Overton (1904) reported that a six-gram tree frog, *Hyla arborea,* after a loss of a third of its weight through desiccation, regained its water at a rate 25 times that of *Triton cristatus* of the same size, or a toad, *Bombinator igneus,* of similar size under the same conditions. He ascribed the tree frog's ability to remain out of water, regaining its evaporated water from dew on leaves, to the great absorbing power of its skin. Scala's (1936) claim of a correlation between rate of water loss and the degree of terrestrialism in amphibians has been discussed in the preceding section. In the same work, the three species whose rates of water loss were measured were also used to measure uptake following desiccation. Of the forms used (species not indicated), the toad, whose rate of loss was slowest, regained water most readily. The salamander, which lost water most readily, had the slowest rate of uptake. The frog was intermediate in both respects. Scala's failure to use animals of comparable size, as in resistance to water loss, also tends to invalidate the measurement of uptake following desiccation. Loss as well as uptake of water was recorded and graphed in grams rather than percent of body weight. As a result, comparisons of individuals as well as species are rather difficult to interpret. Cohen (1952) compared the rates of hydration following desiccation for the same three species of salamanders referred to in the preceding section. Aneides regained body water more rapidly than Ensatina, which in turn recovered more readily than Triturus. Although comparable sizes were not employed, it appears certain that the most completely terrestrial form, Aneides, became rehydrated with the greatest facility of the three species.

To augment the somewhat meager information on comparative rates of water uptake following desiccation, and to test the hypothesis that the rate of uptake is correlated with habitat, a brief study of this subject has been undertaken, employing animals of comparable size throughout. Three species of anurans were compared: *Scaphiopus hammondii, Rana pipiens,* and *R. clamitans.* Five specimens averaging about 20 grams in weight were used in each of the three species, the range of size being from 15 to 25 grams. Before desiccation, all animals used were acclimated for at least 48 hours in the aquarium to which they were to be returned to regain their water following desiccation. Tap water was passed through the aquarium at a steady rate to maintain as constant osmotic conditions as possible. The temperature was adjusted to 22° C, plus or minus one degree, by the proper combination of hot and cold water. A cage with compartments for ready identification of experimental animals was lowered into the aquarium so that the amphibians were completely immersed. Only enough room was left at the surface for emergence of the nares for breathing. After being dried and weighed, the animals were desiccated for the desired time in airflow desiccators. They were weighed again, returned to the proper water compartments, and reweighed hourly to determine the rate of absorption of water. The urine was forcibly pressed from the bladder before desiccation, but not before each subsequent weighing, since the information desired was how much time was required for a quantity of water to pass inward equal to that which passed outward through the skin during desiccation. Whether that absorbed water was retained in the tissues or was partially stored in the bladder before rehydration was completed was immaterial to the present study.

Results of these experiments appear in Figure 2. It is seen that *Rana pipiens* regained its orig-

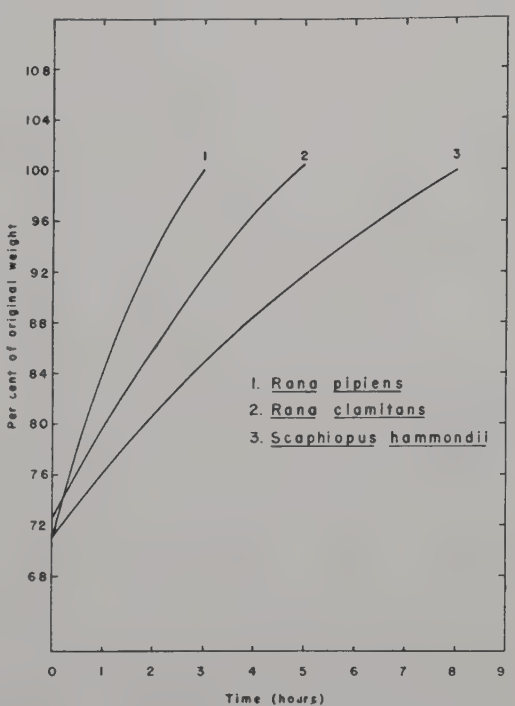

FIG. 2. Uptake of water following desiccation. The graph indicates the average rate at which 5 animals of each of 3 species regained their original weight when returned to water following desiccation to a loss of about 28% of their body weight.

inal weight in an average of three hours and *R. clamitans* in slightly less than five hours, while *Scaphiopus hammondii* required eight hours to recover its initial water content. All three species had been desiccated to a nearly equal average loss of about 27-29% of the body weight.

That the increase in weight of dehydrated amphibians replaced in water is due only to absorption through the skin and not to drinking is virtually certain. The change in rate of uptake shown in Figure 2 is relatively constant, which would be unlikely if drinking occurred. No amphibian of any species was observed to drink water even after extended desiccation. Krogh (1939), Adolph (1943), and Prosser *et al.* (1950) have discussed drinking in amphibians. The conclusion appears to be universal among all observers that drinking does not occur in normal amphibians. Only Overton (1904) observed that frogs drank water and then only when they had been severely dehydrated by immersion in strong salt solutions.

Considering the three species used, there is no apparent correlation between the efficiency of rehydration and the degree of independence of water as reported by Scala. The species least dependent on open water, *Scaphiopus hammondii,* required by far the longest time to regain its lost water. However, of the two species of Rana, the more terrestrial, *R. pipiens,* regained water more rapidly than the aquatic *R. clamitans.* Although there are obviously specific differences in the rate of water uptake following dehyration, and in certain cases, *e.g.* the *Hyla arborea* of Overton's experiments, they may have significance in the habitat selection of the species involved, no general statement can be made that ready rehydration is associated with terrestrialism in amphibians.

The present study fails to substantiate Scala's observation that a species that loses water most rapidly recovers it most slowly. On the contrary, these three species bear the same relationship to each other in the facility with which they recovered water as they do in the rate at which they lost water (Fig. 1).

This observation confirms the view of several recent authors that amphibian skin's permeability to water is the same in both directions. A number of earlier writers reported experiments demonstrating that the amphibian skin has an inward permeability to water which is greater than its outward permeability (Reid 1890; Maxwell 1913; Przyleski 1924). That the skin of normal frogs has an irreciprocal permeability for certain salts and other water-soluble substances appears to be incontestable (Przyleski 1922), and it is well known that salt is actively taken up by frog skin against a gradient (Huf 1936; Krogh 1937, 1938, 1939). However, the irreciprocal nature of the skin's permeability to water has been disproven by Hevesy, Hofer, and Krogh (1935), who determined permeability by the use of heavy water. Their results were confirmed by Rubinstein and Miskinowa (1936) who found that the rates of water transport were the same in both directions if the skin was normal. Rey (1937) also determined that the passage of water through the skin of frogs was a purely osmotic phenomenon, that the direction and speed of osmosis depended solely on physical factors, and that water passed equally readily in both directions. Essentially the same thing was demonstrated earlier by both Durig (1901) and Overton (1904).

It follows that, if permeability to water is the same in both directions, a species which loses water very readily should also absorb water relatively quickly. Similarly, if the skin has developed a detectable degree of resistance to water loss, this decreased permeability to water should be reflected in a slower rate of water uptake. The present results bear out this interpretation, although Scala's findings do not.

If such a direct correlation between the rates of uptake and water loss is of general applicability among amphibians, small specific differences in resistance to desiccation would probably have little effectiveness in habitat determination. Species dehydrated most readily would have the advantage of rapid recovery whereas the benefit derived from a slower rate of water loss would tend to be partially cancelled by the greater difficulty in reabsorption.

Tolerance to Water Loss

Since amphibians lack effective integumentary resistance to evaporation and lose body water rapidly in unsaturated air, they would die very quickly upon leaving water if they were unable to tolerate considerable loss through evaporation. That they can survive the loss of a great quantity of water before death is well known. Edwards (1824) observed that frogs (unidentified) in air survived the loss of as much as 36% of their weight. Kunde (1857) found that frogs died after a maximum loss of about 30% of their weight, and Durig (1901) placed the vital limit at 30-39% (both used unidentified European species). Langlois and Pellegrin (1902) stated that toads (*Bufo vulgaris*) could stand a loss of as much as 49% of their weight. Overton (1904) determined the maximum tolerance to water loss as 30-32% for both *Rana temporaria* and *R. esculenta.* Hall (1922) found that *Rana pipiens* and

Ambystoma maculatum survived a loss of 41% and 47% respectively, and Ueki (1924) placed the vital limit of water loss at 40% for an unidentified European species.

These isolated observations on tolerance to water loss are of interest but of little significance to the problem of the development of terrestrialism in amphibians. They do indicate that these animals possess the ability to survive rather extensive evaporation and thus are not completely restricted to an aqueous habitat because of the lack of a resistant skin.

Thorson and Svihla (1943), by desiccating anurans of ten species, demonstrated the existence of a clear-cut correlation between the degree of terrestrialism and the extent of tolerance to water loss. Two species of Scaphiopus, terrestrofossorial forms, survived a loss of approximately 48% of their weight or 60% of their total body water, whereas the aquatic species, *Rana grylio,* tolerated only about 30% loss of weight or 38% of the total body water. Other species of Rana, Hyla, and Bufo ranged between the two extremes, essentially according to their degree of independence of water. It was proposed, on the basis of this correlation, that the transition to terrestrial life among amphibians may have been made possible to a greater extent by the development of tolerance to water loss than by the acquisition of a resistant skin. This same correlation was hinted at by Langlois and Pellegrin (1902), who pointed out that the toads which survived up to a 49% loss of body weight were more terrestrial than the frogs of Edwards (1824) which survived only a loss of up to 36%. Rey (1937) also found that a correlation existed between habitats and tolerance to water loss. He used five species including both anurans and urodeles, *Rana temporaria, R. esculenta, Triton marmoratus, Salamadra maculosa,* and *Bufo vulgaris.* The first of these, primarily an aquatic species, survived losses of from approximately 32 to 39% of the body weight (39 to 46% of the total water) whereas the last, the most terrestrial of the five species, tolerated losses of from about 46 to 48% of the body weight or about 58 to 61% of the total body water. More recently, Littleford *et al.* (1947) have also confirmed the existence of this correlation, studying the urodeles, *Eurycea b. bislineata, Desmognathus f. fuscus,* and *Plethodon c. cinereus.* Eurycea and Desmognathus both survived average losses of about 18% whereas Plethodon, the most terrestrial of the three species, survived about 26%.

The existence of greater tolerance to water loss in terrestrial forms than in aquatic forms was thus apparently well established and the ecological implication seemed clear. However, it became apparent from preliminary experiments in the present investigation that pronounced differences in tolerance to water loss between individuals of the same species existed and that these differences were related to the size of the animals involved. Such differences would tend to obscure the facts in the three last-mentioned studies and throw some doubt on the validity of the conclusions presented. In none of these reports was the size of specimens taken into consideration, for animals of very diverse size, both within the species and in different species, were used. In all three cases determinations were made of the average total water content of the various species and the results were quite uniform. All species had a water content in the neighborhood of 80% of the total weight, the greatest deviation being 77.5% in *Rana grylio* (Thorson and Svihla 1943) and 81.25% in *Bufo vulgaris* (Rey 1937). It might be reasoned then that because of the uniformity in water content, as well as the probability that in most cases the animals were in the normal adult size range for the species involved, the data presented were sufficiently reliable. Nevertheless, it was decided that a more general study, taking size into consideration, should be made of tolerance to desiccation, as well as a re-examination of its relation to habitat. In addition to size of specimens, the influence of sex, temperature, and rate of dehydration on tolerance to desiccation have also been studied.

The degree of tolerance to desiccation for a group of amphibians under a given set of experimental conditions was determined by desiccating a number of animals, usually from 20 to 40. Only one animal was placed in each air-flow desiccator, and evaporation was allowed to continue for various lengths of time and thus to various degrees of water loss. The limit of tolerance was determined by using only those animals which were judged to have arrived very close to their vital limit when removed from the desiccators. Those animals which lost more water than this group were all dead when removed from the desiccators, while those that lost less were all considered to have been capable of greater loss. Hence, neither group has been used in computing vital limits. In each series, at least eight and usually ten or more animals were used to provide data for the computation of the vital limit. Of this group, all of which were alive when removed from the desiccating chamber, some lived on indefinitely while others survived only for a short time. Those animals which survived for as much as a few hours

after replacement in water regained approximately their original weight and with rare exceptions lived for many days with no apparent ill effects. Since hundreds of experimental amphibians were sometimes desiccated within a few days, difficulties in keeping records on so many animals made it advisable that rehydrated animals be kept under observation only for about 48 hours following desiccation, and survival for that length of time was considered sufficient evidence of indefinite survival.

Influence of Size on Tolerance to Water Loss

To determine the relationship between size of specimen and the degree of tolerance to water loss, *Rana pipiens* of both sexes were used. These were divided into five size groups ranging respectively from 5-14, 15-29, 30-44, 45-59, and 60-74 grams. The vital limit of tolerance was determined for each group. The results are shown in Figure 3.

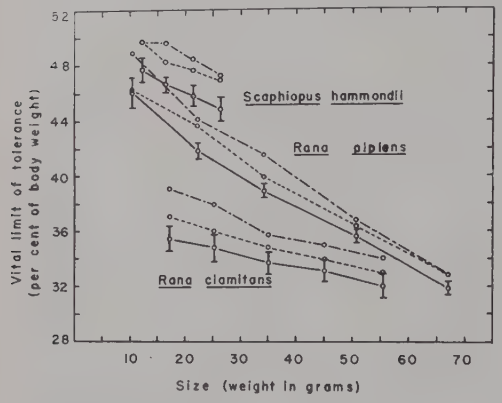

FIG. 3. Influence of size on tolerance to water loss. The 3 means of expressing the vital limits are described in the text. Each average figure represents from 10 to 29 individuals. The reliability of the points is shown by the cross bars, representing plus and minus twice the standard error of the mean (Dice and Leraas 1936).

The vital limit for each group has been expressed in three ways: (1) by determining, for a given group, the highest percentage of body weight lost by any animal which was alive when removed from the desiccator, whether it subsequently survived or not (points connected by unequally broken lines); (2) by ascertaining in that group the highest percentage loss sustained by any one animal which survived the desiccation indefinitely (points connected by regularly broken lines); (3) by taking the average percentage of body weight lost by all the animals of the group which were considered to be very near their vital limit when removed from the desiccators (points connected by unbroken lines). Regardless of which method was used, the variations between the five size groups were essentially the same.

It is seen that the smallest group tolerated losses of about 13 or 14% more than the largest group, and the three intermediate-size groups exhibited rather regularly distributed vital limits, intermediate in value. This difference in tolerance to water loss between the size groups within the species, *Rana pipiens,* is almost as large as the greatest difference between the various species reported by Thorson and Svihla (1943) and larger than that reported by either Rey (1937) or Littleford *et al.* (1947). If the same type of variation existed in the other species, the use of poorly matched sizes in different species could conceivably have led to erroneous conclusions in all three investigations.

When species of comparable size range, selected from the three studies referred to above, are compared, each comparison individually confirms the existence of a definite correlation between habitats and tolerance to water loss. Nevertheless, since each of the three studies included species varying considerably in size as sources of data to support the conclusions, some doubt could reasonably exist as to the validity of those conclusions. It was therefore considered desirable to make a new study of tolerance to desiccation in relation to habitat by using specimens comparable in size in each of the species.

Three species of anurans were selected for these experiments. *Rana pipiens* was used as the intermediate or semi-aquatic species. *R. clamitans* was selected as the most equatic species within the size range of *R. pipiens, and Scaphiopus hammondii,* in spite of a somewhat restricted size range, was chosen as the least aquatic species. *R. clamitans* was divided into five size groups of 10-19, 20-29, 30-39, 40-49, and 50-59 grams respectively. Four groups of *S. hammondii* ranged from 9-13, 14-18, 19-23, and 24-28 grams. The vital limit of water loss was determined for each group in the same manner as for *R. pipiens* and the data expressed in the same three ways as previously described.

The results shown in Figure 3 indicate not only that the tolerance to water loss in all three species is greater in small animals than in large ones, but also that the same correlation between degree of tolerance to water loss and habitats as was reported by Rey, Thorson and Svihla, and Littleford *et al.,* does exist even when specimens of the same size in each of the species are compared.

The significanc of the differences between means is indicated in Figure 3 by the plotting, for each

mean, of plus twice the standard error of the mean and minus twice the standard error of the mean according to the method of Dice and Leraas (1936).

The greater initial water content of the smaller animals was thought to be a possible explanation for the greater tolerance to water loss in small amphibians than in larger ones. The decrease in body-water content associated with aging is a well known phenomenon among animals in general, although not very well documented in the case of amphibians. A number of papers dealing with water content of larval amphibians have been reviewed by Rey (1937). Rey has himself shown that in *Rana esculenta,* tadpoles, before the apperance of external limb buds, had a water content of 92% and that the proportion of water diminished to 84% in the fully metamorphosed frogs. He also demonstrated that the diminution of water content continued at a reduced rate after metamorphosis, the oldest animals having a water content of only 80.5%. However, Rey, in his determination of the limits of tolerance to water loss, noted no difference in tolerance correlated with age and so did not associate difference in water content with the latter phenomenon. Other previously mentioned investigators who determined tolerance to water loss, if they quoted figures for total water content, used average figures for the species concerned and made no mention of the relation between size and water content.

Using the same three species as above, an investigation was made to determine whether any relationship existed between water content and tolerance to water loss at different size levels (or different ages, for growth is continuous in amphibians). A number of animals (92 *Rana pipiens,* 63 *R. clamitans,* and 47 *Scaphiopus hammondii*), representing the full size range of each species, were completely desiccated in an oven thermostatically controlled at 105° C. Desiccation was continued until the body reached a constant weight, usually at least four days being required. The results are shown in Figure 4.

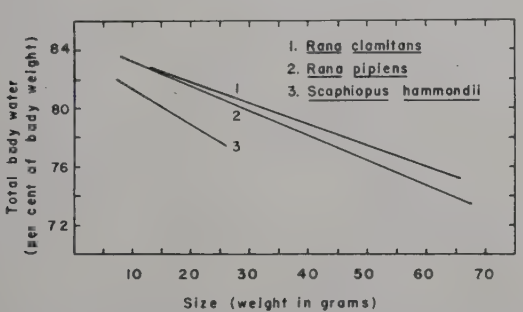

FIG. 4. Relationship of size to total body water. Total water content was determined by complete desiccation at 105° C.

It is evident that a decided difference in body water content exists between small and large animals of all three species. The degree of difference corresponds well with Rey's figures for *Rana esculenta* although he used a more restricted size range.

It is also obvious that in all three species the extremes of difference in water content correspond fairly closely with the differences in degree of tolerance to water loss. It appears certain therefore that the greater tolerance to water loss in small amphibians is directly related to the greater amount of initial water present.

The possibility that differences in water content might also explain dissimilarities in tolerance to desiccation which exist between various species of amphibians is not supported by the data in Figures 3 and 4. It is apparent that *Scaphiopus hammondii,* with the highest tolerance to water loss, has a lower water content than frogs of equal size in either of the other two species. Conversely, *Rana clamitans,* with the highest water content of the three species, can survive less loss of water than either of the other two.

Since small amphibians have a higher tolerance to water loss than large ones, it might be inferred that the small animals are better adapted for living out of water than larger ones. If this one factor were considered alone, the assumption would probably be true. However, as noted previously, small animals lose water more rapidly than large ones because of the relatively greater body surface in the former. Examination of Table I discloses that in all three species, the smallest group reached its limit of tolerance in a shorter time than the largest group, in spite of the fact that the smaller animals had farther to go before reaching that vital limit. Therefore, the advantage gained by virtue of a high tolerance to water loss in small animals is more than offset by the disadvantage of a faster loss of water due to a relatively greater body surface exposed to evaporation.

Influence of Sex on Tolerance to Water Loss

Rey (1937) reported that sexual differences in general water metabolism were not evident in amphibians, although the water content of females during the breeding season was slightly higher than in males because of the large mass of eggs present. Observations made by the writer confirm those of Rey. Nevertheless, because of lack of

TABLE I. *Time required to reach the vital limit of water loss*

Weight (grams)	No. of specimens	Average time	Ave. vital limit (% of orig. wt.)
A. *Rana pipiens*			
5-14	10	9:40	46.0
15-29	24	13:39	41.8
30-44	29	16:27	38.9
45-59	10	18:53	35.6
60-74	10	20:14	31.9
B. *Rana clamitans*			
10-19	20	10:58	35.5
20-29	14	13:53	34.8
30-39	12	16:22	33.7
40-49	10	18:25	33.1
50-59	10	19:58	32.0
C. *Scaphiopus hammondii*			
9-13	13	17:01	47.7
14-18	21	19:04	46.6
19-23	14	20:43	45.8
24-28	11	22:07	44.8

precedent in studies on tolerance to water loss, it was thought advisable to determine the vital limit of tolerance in both sexes.

The data used for determination of the limit of tolerance for *Rana pipiens* of 30-44 grams in the preceding section were separated into male and female series and the vital limit of each group was determined. The 10-19 gram series of *R. clamitans* was separated according to sex and treated similarly. *Scaphiopus hammondii* was not analyzed since too few females were available to make a valid comparison. The results are summarized in Table II for the two species studied.

TABLE II. *Influence of sex on tolerance to water loss*

Species	Sex	No. of specimens	Average time	Ave. vital limit (% of orig. wt.)
Rana pipiens....	male	15	16:32	39.0
Rana pipiens....	female	14	16:22	38.8
Rana clamitans..	male	6	11:00	35.9
Rana clamitans..	female	14	10:57	35.3

It is seen that in both species, when males and females of similar size are compared under identical experimental conditions, the vital limits of water loss are very nearly identical. Application of the *t* test of Fisher (1935) proved the slight differences to be negligible. Therefore, in all other determinations of vital limits of tolerance to water loss, sex, although recorded, has not been taken into consideration.

The time column of Table II also indicates that the rate at which water was lost from the body surface by evaporation was nearly identical in males and females of both species.

Influence of the Rate of Desiccation on Tolerance to Water Loss

The limits of tolerance to water loss cited by earlier investigators have varied from about 30% of the body weight to nearly 50%. Much of this variability is no doubt due to the difference in species used for experimentation, and some variation has undoubtedly resulted from difference in size of experimental animals used. However, Rey (1937) ascribed the variability primarily to differences in the rates of desiccation employed. He noted that some of the investigators used calcium chloride or other chemical desiccators which dried the amphibians much more slowly than the air-flow desiccators used by others. He reported experiments in which frogs dehydrated in deep glass bottles with no air flow survived two or three days to a loss of 33-38% of their weight, whereas animals dehydrated by exposure to a current of air from a fan died in a few hours after losses of only 21-26%. He concluded that the limit of dehydration varied inversely as the rate of dehydration. Kunde (1857) and Durig (1901) both noted earlier that frogs died after a loss of about 15% of their weight if the evaporation was rapid, whereas about twice this loss could be sustained if it was slow. Almeida (1926) also stated that death occurred after a smaller loss of water during rapid desiccation than during slow desiccation. The methods used by these authors varied and were all of such an indefinite nature that it was impossible to compare exactly the degree of severity with which the animals in the present work were desiccated with those of Kunde, Durig, Almeida, and Rey.

In order to place on record a more concrete and exact analysis of the effect of the rate of desiccation on the limit of tolerance to water loss, *Rana pipiens* of 15-30 grams weight were desiccated at various rates and the vital limit of water loss at each rate was determined in the same way as described earlier. The desiccation was carried out at room temperature with the air flow adjusted at one, two, four, eight, and twelve liters per minute through the standard 3.6-liter desiccating jars. In addition, another group was desiccated at zero flow in calcium chloride desiccators. A final group was desiccated in ordinary room atmosphere of about 50% relative humidity (determined by a wet and dry bulb thermometer) in the path of a strong air current from an electric fan. The air flow used for the latter series was too massive to be measured in terms of the other

groups, but should be roughly comparable with that used by Rey, Kunde, and Durig for rapid desiccation. Likewise, the series desiccated in calcium chloride jars should be fairly comparable with the animals desiccated at slow rates by the same investigators. From 8 to 17 frogs were desiccated in each series.

The results are shown in Figure 5. It is apparent that the present findings confirm those of previous authors only as far as the latter went. At an extremely rapid rate of desiccation (using the electric fan) the vital limit of water loss is conspicuously lower than at the very slow rate accomplished in calcium chloride jars. However, Rey's statement that the limit of tolerance varies inversely as the rate of desiccation does not appear to be justified. The results of the present experiments indicate that the vital limit diminishes in both directions from an optimum rate of air flow, which under the present experimental conditions is eight liters per minute through 3.6-liter jars.

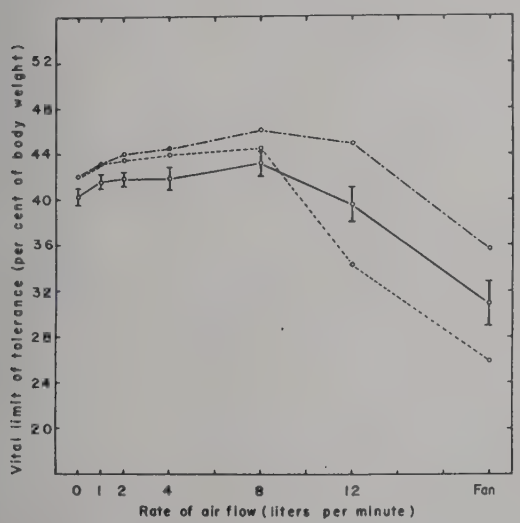

FIG. 5. Influence of the rate of desiccation on tolerance to water loss. The 3 means of expressing the vital limits and the demonstration of statistical validity are the same as those described for Figure 3.

At all rates of flow from zero through eight liters per minute, there were no permanent ill effects apparent in frogs that survived the desiccation. They regained approximately their original weight and behaved as normal undesiccated frogs. However, those that survived the desiccation at 12 liters per minute or with the electric fan, although they re-absorbed water rapidly, at least to their original weight, and under other conditions should have been expected to survive indefinitely, almost invariably suffered severe after-effects. They did not survive for more than 24 hours except when they had lost less than 34.7% in the 12-liter-per-minute group and 25.9% in the group desiccated by means of the fan.

The more severely desiccated frogs that survived the two most rapid rates of evaporation for 12-24 hours, usually followed by a recovery of at least their original weight, were characterized by certain symptoms which apparently contributed to their death. The skin remained red in spots and blistering occurred, especially on the thighs. The frogs became edematous, often regaining several grams more than their original weight, and frequently exhibited a lack of coordination of body movements.

Apparently, at the slower rates of water loss, the water lost superficially is replaced from that deeper in the body at a rate rapid enough to prevent serious damage to the skin. When evaporation is very severe, transport of water from deeper tissues is apparently not rapid enough to replace that lost by evaporation, and surface tissues are injured. The edematous condition may be caused directly by impairment of renal function or indirectly by an upset of secretion of the water balance principle of the neurohypophysis. Possibly damage to the central nervous system results in the loss of coordination. Although it is not difficult to understand how rapid evaporation could injure the surface of the body, it is not clear why the kidneys, neurohypophysis, or central nervous system would be more seriously affected by rapid than by slow water loss, since all these structures are located well below the outer surface.

Since water loss was not rapid enough to bring about serious side effects in the groups of frogs desiccated at rates eight liters per minute or slower, an explanation for the decrease of the limits of tolerance associated with slower desiccation must be sought elsewhere. The length of time required to reach the limit of tolerance to water loss varied inversely as the rate of desiccation. The animals desiccated by means of the electric fan reached their vital limits in an average time of one hour and 48 minutes. Those desiccated in a flow of 12 liters per minute required three hours and 50 minutes; eight liters, 8:05; four liters, 11:19; two liters, 13:27; one liter, 18:47; no air flow, 31:36. During the course of desiccation, the animals are forced to tolerate certain unfavorable physiological conditions. The loss of water presumably increases the viscosity of the blood, throwing an extra burden on the heart and slowing the transport of oxygen, carbon dioxide, and other substances. The suspension of kidney

function after the early stages of desiccation (Adolph 1927; Rey 1937) undoubtedly results in the accumulation of excretory products, possibly to a toxic concentration. Physiological processes within the cells are also likely to be affected unfavorably by the great change in water content which occurs at advanced stages of desiccation. It seems very probable therefore that a long exposure to drying would tend to result in death after a smaller loss of water than a short exposure to more rapid drying, at least up to a limit. Under the present experimental conditions, that limit seems to be eight liters per minute, beyond which deleterious after-effects cancel the advantage gained by further reduction of exposure time.

To supersede Rey's statement of an inverse relationship between the limit of tolerance to desiccation and the rate of water loss, it can be stated that, in *Rana pipiens*, an optimum rate of water loss exists. This is determined under a given set of experimental conditions by the duration of the desiccation and the ability of the animals to replace water loss from the surface by that from deeper tissues at a sufficiently rapid rate. At rates slower than the optimum, the vital limit decreases, possibly because of increased duration of exposure to unfavorable physiological conditions, while at rates above the optimum, the vital limit also decreases due to the harmful effects of too-rapid drying.

Influence of Temperature on Tolerance to Water Loss

Although the influence of temperature on the rate of evaporation is well known, and the rate of water loss in amphibians is directly affected by temperature, to the writer's knowledge nothing has been published concerning the effect of temperature on the vital limit of water loss in amphibians.

A series of experiments was designed to ascertain whether temperature had an influence on tolerance to desiccation, and if so, to what extent. For these experiments, *Rana pipiens* of 30-35 grams weight were used. A series of from 8 to 13 frogs was desiccated at each of eleven temperatures ranging, at five-degree intervals, from 5 to 50° C, and in addition, a series was run at 52.5°. The vital limit of tolerance to desiccation was determined for each group in the usual manner. All the experiments were conducted in an incubator in which the temperature could be kept constant, with a variation of not more than one degree plus or minus. At temperatures below that of the laboratory (20° and below), a cold room was utilized in which the temperature was maintained at about four degrees. Because of the limited space available in the incubator, and other technical difficulties, the air-flow desiccators could not be used. In their place, the calcium chloride desiccators described previously were employed.

The evaporation of water requires energy, which in the present situation was drawn from the metabolic heat of the frogs being desiccated. Thus, the temperature of the experimental animals was lower than the air in the desiccator. The depression of the frogs' temperature was sufficient to lower the temperature inside the desiccator to a point appreciably lower than that of the air in the incubator. It was therefore considered advisable to determine the temperature of the frogs at each incubator temperature as well as that of the air inside the desiccator, since the latter was actually the frog's environmental temperature rather than the temperature at which the incubator was set. The temperatures were taken by means of a thermocouple used in conjunction with a potentiometer indicator. Frog body temperatures were taken cloacally. Table III shows the divergence of the temperatures of frogs and desiccators from that of the incubator. The difference between the temperature of the incubator and the desiccator ranged from 2.5° at an incubator temperature of 52.5° down to only 0.3° at the lowest temperature (5°), while the depression of the frog's temperature below that of the desiccator was 13.2° at the highest temperature and only 1.3° at the lowest. The lower differential at reduced temperatures was due to the slower rate of evaporation at low temperature levels.

The results of these experiments (Fig. 6) indicate that the vital limits of water loss are not affected to a great extent by temperature within the range of normal summer environmental temperatures of most North American species, *e.g.*,

TABLE III. *Influence of temperature on time required to reach vital limit of water loss; divergence of temperature of frogs and desiccators from that of incubators*

Temperature (°C)			No. of specimens	Average time	Ave. vital limit (% of orig. wt.)
Incubator	Desiccator	Frog			
5	4.7	3.4	13	99:11	30.6
10	9.2	7.2	11	103:23	38.6
15	13.8	11.9	11	65:02	39.8
20	18.8	14.8	10	42:53	40.2
25	23.1	19.3	10	30:08	40.2
30	28.2	22.6	12	18:00	39.4
35	33.4	26.4	10	11:33	38.6
40	38.3	29.1	10	9:26	36.8
45	43.2	31.2	12	5:10	31.1
50	47.7	35.0	8	3:17	26.7
52.5	50.0	36.8	8	0:36	5.8

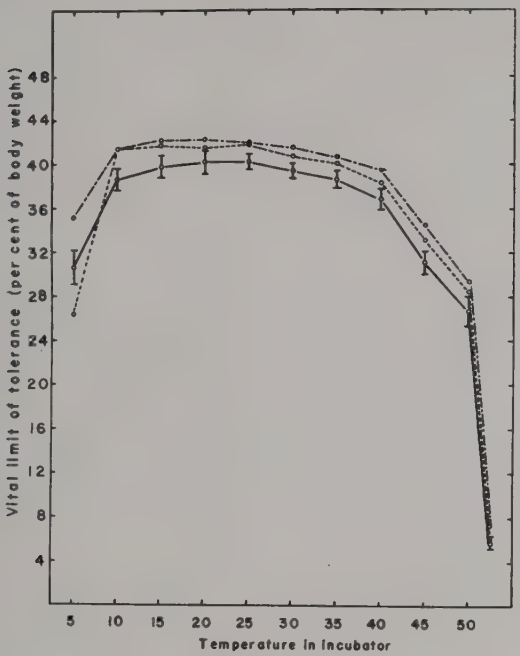

FIG. 6. Influence of temperature on tolerance to water loss. The 3 means of expressing the vital limits and the demonstration of statistical validity are the same as those described for Figure 3.

from 10 to 40° (incubator temperatures). The greatest difference in vital limits within this range is not much more than 3% of the body weight. Within this broad range there is a slightly more definite optimum at 15-25° within which there is scarcely any difference in vital limits. However, temperature does have a marked effect on the time in which the vital limit is reached (Table III). At temperatures from 10 to 40° (incubator), in which range the vital limits are quite comparable, the time taken to lose a lethal percentage of water varies from more than four days at 10° to only about nine hours at 40°. Therefore, considering both the limit of tolerance to desiccation and the speed of reaching that limit, the survival capacity of frogs on land would probably be greatest at from 10 to 15°.

Although within its normal range temperature has little effect on the vital limit of water loss, at both high and low extremes of temperature, the limit of tolerance falls off abruptly.

Considering first the low extreme, five degrees, an explanation was sought for the lower vital limit in the long period of exposure to desiccation. In the preceding section, it was seen that the group of frogs desiccated with zero air flow required more than 31 hours to reach their limit of tolerance at room temperature. It was thought that their somewhat lower vital limit was due to their longer subjection to desiccation than the frogs exposed to eight liters per minute flow, whose vital limit was three or four per cent higher. The frogs desiccated at five degrees required an average of about 99 hours to reach their vital limit. However, the ten-degree frogs were under desiccating conditions even longer (ave., 103 hours) and yet could tolerate a greater loss of water than those at five degrees. Therefore, the time element does not appear to be the sole determining factor in this case, although it may contribute to the lowering of the vital limit. Very likely, the lower rate of metabolism at depressed temperatures makes it possible for the amphibians to survive longer periods of desiccation than at higher temperatures.

The possibility appears that the low temperature itself might be responsible for the death of the frogs rather than the loss of water. However, frogs placed in ice water (nearly zero degrees) survived for many days and showed no ill effects when returned to room temperature.

At the high temperature extreme (above 40°, incubator temperature) a decided lowering of vital limit appears as the temperature rises, with a very sharp drop occurring above 50°. The sudden drop between 50° and 52.5° suggested that death at the highest temperature was perhaps due to the elevation of the body temperature beyond the level of temperature tolerance rather than to reaching the limit of tolerance to water loss. At 52.5°, only an average loss of 5.8% of the body weight was sustained and death ensued after an average of only 36 minutes. At normal temperatures a loss of 5.8% has no visible effects on frogs. They remain active and the skin stays moist after a far greater loss than this. It is inconceivable that such a comparatively slight loss of water could contribute to the death of the animals in more than a very incidental manner.

To test the hypothesis that temperature tolerance rather than tolerance to desiccation was the limiting factor at high temperatures, groups of 10 frogs each were plunged into water maintained at various temperatures from 34 to 45°. The frogs were kept in the water for a period of one hour with no previous acclimatization. Table IV shows that at 36°, six frogs survived and four died within the hour. Below this temperature, all frogs survived, but at all higher temperatures, they all succumbed in an increasingly short period of time as the temperature increased. At 37°, all died within 40 minutes. It was seen (Table III) that the frogs desiccated at 52.5° died after an average of

TABLE IV. *Temperature tolerance of* Rana pipiens *in water*

Temperature, °C	Number that died (of ten)	Time for death
	Exposed for 1 hour	
34	0	All survived
35	0	All survived
36	4	20, 25, 30, 35 minutes (six survived)
37	10	10 to 40 minutes
38	10	5 to 15 minutes
39	10	3 to 6 minutes
40	10	2 to 4 minutes
45	10	1½ to 2½ minutes
	Exposed for 3½ hours	
34	0	All survived
35	5	2 to 3 hours
36	10	½ to 2 hours
37	10	10 to 45 minutes
	Exposed for 5½ hours	
30	0	All survived
31	0	All survived
32	0	All survived
33	0	All survived

36 minutes, and in no case did one of these survive more than 40 minutes. The average body temperature of these frogs was 36.8°. It therefore seems certain that the apparent drop in vital limits of water loss noted in Figure 6 at 52.5° is in reality a result of the frogs' arrival at their limit of temperature tolerance.

When the incubator temperature was 50°, the body temperature of the frogs averaged 35° (Table III), and they survived an average loss of 26.7% of their body weight, which was lost in an average period of three hours and 17 minutes and in no case more than three hours and 55 minutes. Several series of 10 frogs each were immersed in water at temperatures ranging from 34 to 37° and kept there for three and one half hours. At the end of this period, Table IV shows that, of the group placed in water at 35°, half survived, while at 36°, all died before the end of the three and one half hours. The frogs desiccated at 50°, with average body temperature of 35°, died slightly before the body temperature reached the level that was invariably lethal (36°). The water loss in this case was 26.7%, a considerable loss, although one easily endured at normal temperatures by *Rana pipiens* of the size range employed (30-35 grams). It appears probable then that death at 50° (incubator temperature) was caused by a combination of having reached the limit of tolerance to high temperature as well as of water loss.

As a control on the 45° group, whose average body temperature was 31.2°, and which survived an average of five hours and 10 minutes and a loss of 31.1%, series of 10 *Rana pipiens* each were placed in water at temperatures from 30-33° for five and one half hours. None of these frogs died, indicating that the vital limit of water loss shown in Figure 6 for 45° was indeed primarily an expression of tolerance to water loss rather than to high temperature although the relatively high temperature probably had some influence in the lowering of tolerance to desiccation.

SUMMARY

The most common approach to the problem of amphibian water metabolism has been through the study of animals in the water. The present investigation concerns the relationship of water economy to the development of terrestrialism in amphibians. In making a transition from the aquatic to the terrestrial mode of life the efficiency of water exchanges in the atmosphere would appear to be more critical than features of the water metabolism of the animals in a water medium. The approach to the problem has therefore been through a study of various aspects of the water economy of amphibians in air, as determined by desiccating the animals under carefully controlled conditions.

No species studied exhibited an important degree of resistance to drying. Slight interspecific differences in resistance were noted, but no correlation existed between the resistance of the skin to water loss and the degree of independence of water. The claim that species with rough, dry skins lose water more slowly than those with smooth, moist skins, and thus are better adapted for a terrestrial life, was not supported. It does not appear that the development of resistance to desiccation has been an important factor in the appearance of terrestrialism among amphibians.

In certain species reported in the literature a rapid rate of water uptake following dehydration may have been of adaptive value in occupying a dry habitat. However, on the basis of present results, no broad statement can be made that rapid rehydration following desiccation is associated with terrestrialism in amphibians in general. Contrary to published accounts, in the species studied, those that lost water most rapidly also recovered it most readily while those that lost slowly reabsorbed water slowly. This observation is in agreement with the generally accepted view that the permeability of amphibian skin to water is directionally reciprocal.

It was demonstrated that small amphibians had a greater tolerance to water loss than large ones. This was shown to be related to the fact that small amphibians have a greater body water content than

large ones, for the difference between large and small animals in water content corresponded quite closely with the difference in the relative amount of body water loss that could be tolerated. When the tolerances to water loss of three species of anurans of diverse habitats were compared, taking size into account, earlier findings were confirmed that great tolerance to water loss is correlated with a high degree of terrestrialism. The extent of differences in tolerance and the close correlation of tolerance with habitats suggests that the acquisition of increased tolerance to water loss has probably been an important factor in the development of terrestrialism in amphibians. The interspecific differences in tolerance were shown to be independent of small interspecific differences in water content. The advantage gained by virtue of a high tolerance to water loss in small amphibians is counteracted by the disadvantage of a more rapid rate of water loss because of the relatively greater body surface exposed to evaporation.

The degree of tolerance to water loss as well as the rate of water loss was almost identical in both sexes.

Previous investigators have stated that the degree of tolerance to water loss in a given species varies inversely as the rate of desiccation. This statement was not supported by the present results. It was found that an optimum rate of water loss exists. At rates slower than the optimum, the limit of tolerance is lower, possibly because of increased duration of exposure to unfavorable physiological conditions. At rates much more rapid than the optimum the limit of tolerance also drops, probably as a result of deleterious after-effects resulting from the inability of the animals to replace water lost superficially by that from deeper tissues at a sufficiently rapid rate.

The limit of tolerance to water loss was not affected to a great extent by temperature within the broad range of normal summer environmental temperatures of most North American species of amphibians. However, at both high and low extremes of temperature the limit of tolerance fell off abruptly. At low temperatures, slower evaporation, with the consequent prolongation of exposure to unfavorable physiological conditions, probably contributed greatly to the decrease in tolerance. As the temperature rose, a point was reached where the limit of temperature tolerance became the critical factor rather than tolerance to water loss.

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TITUS SMITH, A PIONEER OF PLANT ECOLOGY IN NORTH AMERICA

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The contribution of the early naturalists to plant ecology is seldom acknowledged, though many of the facts upon which ecology is based were observed and correctly interpreted long before the subject became established professionally. In calling attention to the neglected yet brilliant investigations of Titus Smith, Jr., the writer hopes both to rescue from undeserved oblivion one of the earliest North American ecologists, and at the same time to provide an example of the marked capacity for careful observation and induction exhibited by many of the early amateurs.

Titus Smith, Jr., born in 1768 and died in 1850, was a native of New England who accompanied his father to Halifax, Nova Scotia, in 1783. After a broad education at home, he became a land surveyor, and in 1801 was commissioned by the governor of the colony to make a survey of the unfrequented areas of Nova Scotia, for the purpose of describing their natural resources, agricultural potentialities, and suitability for settlement. During 1801 and 1802 Smith made three trips, to the eastern, western, and northern parts of the Nova Scotian mainland, largely through the woods and with a single companion (none on the northern tour). The unpublished journals of these tours, together with a map, lists of the flora, and notes on the various tree species, provide an admirable description of the interior of the province at that time, and are deposited in the Public Archives of Nova Scotia. Their importance to geographers of northeastern America has recently been emphasized by Clark (1953 and *in press*). While they also contain much material of value to ecologists interested in Nova Scotian vegetation, it was in a later paper, published by Loudon in the Magazine of Natural History for 1835, that Smith presented the ecological theories which must have had their origin in his observations on the governor's survey. Since the above journal is unlikely to be widely available, frequent and extensive quotation can alone do justice to what may well be the first major contribution to plant ecology in North America.

Plant Successions

Succession has of course long been recognized and described by naturalists (*cf.* Clements 1916, Deevey 1942, Spurr 1952, Gorham 1953). However, for wideness of scope and clearness of appreciation, Smith's account can hardly be rivalled, either in America or Europe. We may begin by considering the changes following disturbance of the forest by storm, fire or man. Of the hardwood forests he writes[2]: "This portion of the forest can rarely be affected by fires, as the leaves in summer are full of watery juices. Should a part of it be overthrown by a hurricane, it is very soon replaced. Shoots from the old roots and seedlings spring up, among which a few scattered plants

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The writer wishes to thank Professor D. C. Harvey, Provincial Archivist of Nova Scotia, for informing him of the existence of Smith's unpublished MSS. He is also grateful to Professor Andrew H. Clark of University of Wisconsin, who has provided a copy of the transcribed MSS.

[2] The quotations to follow have been abridged wherever possible without loss of meaning, and are all from the paper of 1835. Smith's plant names are elucidated in an appendix.

of the balsam fir (*Abies balsamifera* Mx.) appear, which, overtopping the hardwood, by their shelter accelerate its growth, and, being short-lived trees, are in their turn, overtopped and suffocated by the hardwood, when it no longer needs their assistance." In contrast, however: "Whenever a growth of hardwood, on a poor soil, is cut down, the land burnt over, and exposed for several years to pasturage, it will, if left undisturbed, grow up with a mixture of fir and spruce." In the case of evergreen forests, Smith implies an origin from heathy barrens: "When the woods of fir become so thick that the kalmia perishes, the soil generally becomes covered with various kinds of dry moss. As this vegetable is not quickly decomposed, it forms a portion of the turf, and it assists in preventing its decomposition by excluding the light and air; and securing it from sudden changes in the temperature; as may be proved by the late period at which ground covered with it freezes in winter and thaws in spring." These woods are claimed to be much exposed to fire, the easily inflammable moss spreading the blaze to the resinous branches of the conifers. The consequences are: "The leaves and small spray of the branches are consumed, together with the litter which covered the surface. The naked black surface is now exposed to the sun, and putrefaction commences in earnest, affecting the turf as well as the roots of vegetables which have been killed. The increased temperature brings into action the vegetative powers of seeds which had lain dormant for centuries; raspberries spring up in abundance, together with red-berried elder, birdcherry, sumach, prickly aralia (*?Aralia spinosa*), and the evergreen fumitory. The French willow (*Epilobium angustifolium*) and the cacalias soon find out their favorite light soil. Tracts of a hundred acres are thickly covered by raspberries, loaded with a luxuriant crop. The low barren levels overspread with blueberries; and large tracts occupied by the French willow, together with the large clusters of the scarlet elderberry; altogether give an idea of fertility which forms a remarkable contrast with the sterile appearance previous to the fire.

Within three years this fertility disappears; the turf is greatly reduced in quantity; the land becomes hard and cold, presenting that exhausted appearance which always follows the raising of crops on a burnt soil. Shoots from the white maple (*Acer dasycarpon* Ehrh. syn. *eriocarpon* Mx.) (the roots of which are never killed by fires), brakes, sweet fern (*Comptonia asplenifolia* H.K.), dwarf willows, and withrod, occupy the ground, presently followed by alder; and, when they have formed a sufficient shelter, the firs again spring up, mixed with white birch (*Betula populifolia* H.K.) and poplars. In the lower and more barren tracts the blueberry (*?Vaccinium ?venustum* H.K.) is, by degrees, overgrown by the kalmia and rhodora (*Rhodora canadensis* L.), which are in their turn overtopped by the alder, soon followed by a growth of firs. A number of plants whose seeds never vegetate during the fertile period now appear; the mayflower, the trailing evergreens (lycopodiums), snakeroot (*Aristolochia Serpentaria* L.), mitchella (*Mitchella repens* W.), linnea (*Linnaea borealis* Gron.), pigeonberry, mountain tea (*Gaultheria procumbens* L.), maidenhair (*Adiantum pedatum* L.),[3] several kinds of aster, and goldenrods (*Solidago*). The mosses follow, and the thicket, in thirty or forty years, resumes nearly its former appearance, except that the trees are smaller, and the balsam fir forms a larger proportion of the wood. This tree of rapid growth covers the spruce from winds, and prevents it from forming strong lateral branches, till, having reached the height of 30 ft. or 40 ft., it is overtopped and suffocated by it. When a very old growth of hemlock (*Abies canadensis* Mx.) and spruce has been destroyed by fire, sometimes a growth of beech (*Fagus sylvatica* L. and *ferruginea* L.), birch, and maple takes its place. It also sometimes happens that when an old grove of pine is destroyed, it is replaced by white (*Betula populifolia* H.K.) and yellow birch (*Betula excelsa* H.K.) and oak. But these changes are less frequent than is imagined. Most hemlock woods, when killed by fires, are at first overgrown with birch hooppoles, mixed with firs; but, when the birch has reached the height of 20 ft. or 30 ft., it turns mossy, and continues stationary for perhaps twenty years, during which a young growth of hemlock again springs up, and most of the birches perish. In a similar way, the pine woods, when killed, are first covered with alder, followed by white birch, poplars, and a little oak; but these trees rarely reach any considerable size before they are overtopped by spruce and hacmetac, which is, finally, again mixed with pine."

Later on Smith continues his discussion of nurse plants, by denoting the principal forest trees of the area and pointing out the roles of other plants in bringing them to ascendency. The principle of autogenesis is further explored in the descriptions of succession on bare ground: "The lichens and mosses are necessary to the other plants of barren soils: they prevent the ground from freezing early, or to a great depth, and from thawing

[3] Obviously an error, in the MSS maidenhair is *Vaccinium* (now *Gaultheria*) *hispidulum*, a much more likely plant in such sites.

easily." The effects of frost-heaving are thus minimized. Where this does occur, especially on barren soil, "The *Lichen ericetorum* serves to heal breaches in the green coating of the earth. Upon this crust caribou (reindeer) moss, and other lichens spring up, soon followed by hawkweed, goldenrod, kalmia, and alder." A lucid exposition of xerosere development follows: "The family of lichens appear to derive their nourishment from the air alone. These vegetables serve to introduce soil upon hills of naked rock. It is at first overspread with the crustaceous species; these are followed by the leafy kinds: when they decay their bulk is little diminished. As soon as an inch of turf is formed, the caribou moss appears. A small portion of the rock is changed to sand by the action of the turf. The Acadian heath (*Ceratiola ericoides* L.) and the *Potentilla tridentata* finally spring up, followed, as the turf increases, by black whortle, candleberry myrtle, and other shrubs. The small long-limbed Hudson's Bay pine (*Pinus Banksiana* Lamb.) is usually the first tree on these shallow soils."

The hydrosere also comes in for detailed attention: "Wherever the soil is so poor that turf is formed on the upland, peat earth is formed in the swamps and bogs, generally, in situations that have formerly been ponds or shallow lakes." A good deal of the peat is believed to come from erosion of the upland turf and litter after fires. When the basins are nearly filled with mud mat formation takes place: "The *Andromeda calyculata* is the first shrub that grows upon it; bog moss with Indian cups follows, and the Indian tea, rosemary-leaved kalmia (*Kalmia glauca* L. var. *rosmarinifolia* Ph.), Dutch myrtle, and other bog plants and shrubs, coming in, with a sprinkling of the tough-rooted cotton grasses and sedges, a strong turf is formed, which alternately floats or rests on the mud. When the water sinks below its surface, as it generally does in dry weather, in swamps which have *large* streams running through them, the upper layer changes to a kind of mould capable of producing grass and alder, and the swamps become natural meadows, which are mostly poor on stony vitriolic soils, but better where the upland is a sandy loam, because a portion of it is always carried by rains into the swamps; while on the rocky soils scarcely any earth is mixed with the vegetable matter. These deposits on granite soils are collected in basins formed by the rock; but on the vitriolic soils, where the peat is most abundant, the soil is rendered impervious by slate clay mixed with ochre. The wet peat having the property of changing the slate to clay, considerable quantities of vitriol[4] are contained in the water which enters peat bogs, but it is immediately decomposed. Ochre is always deposited where a rill of vitriolic water enters the swamps: the sulphur probably unites with the peat, as the water runs from the swamps soft and free from vitriol, but usually holding a little carbonaceous matter in solution."

The swamps are also envisaged as a source for reforestation: "The swamps, which escape the fire always, together with the different species of fir, contain alder. This shrub, producing abundance of light seed, which is spread far and wide by the winds, usually composes the greater part of the first growth upon bleak naked hills. When the shrubbery of alder attains the height of 3 ft. or 4 ft., the firs always begin to appear. All the trees of the fir kind are, as well as the alder, furnished with winged seeds."

Another theory elaborated by Smith concerns the anthropogenic origin of heathland: "The great influx of inhabitants in 1783 produced a complete change in the forest. The fires necessary for clearing the land were communicated to the spruce thickets. The profusion of herbage which followed, for a time furnished pasture. This failed in three or four years. The next dry season the fire was rekindled, for renewing it, which it would do in a less degree. Raspberries, French willow, and other vegetables, would appear, but of inferior growth. The roots of the spruce and balsam fir spread horizontally, and take but slight hold of the ground. Being loosened by the sinking of the turf, they are overthrown in every wind, and furnish fuel for successive fires, usually rekindled every dry season till, the combustible matter being consumed, with the exception of that portion washed by rains into the swamps, the ground becomes so much exhausted, that it produces only a growth of heathy shrubs, among which the kalmia predominates; and, in many places, it is necessary that this should continue long enough to form a few inches of turf, before the alder and other large shrubs can be reproduced, as a shelter for another growth of firs.

Near to the cultivated districts, the wood becomes scarce; and the swamps are finally attacked, thus destroying the trees which used to furnish seeds: and it is probable that, at no very distant period, many large tracts will present nearly the same appearance as the naked heaths and downs of the old world.

Although the kalmia burns freely in a dry season, it does not seem possible to destroy it by fires where the surface is covered with broken stones.

[4] Vitriol and sulphureous iron pyrites are terms used interchangeably by Smith.

After it is burnt off, a growth of whortles (*Vaccinium* sp.) often springs up, and bears a plentiful crop for two or three years; but it is finally overpowered by shoots from the roots of the kalmia. It disappears, however, where the turf is completely burnt off from sand or gravel, and is replaced by a growth of lower or trailing shrubs. These are the uva-ursi, the crakeberry heath (*Empetrum nigrum* L.), the yellow-flowering cistus (*Hudsonia ericoides* L.), Acadian heath (*Ceratiola ericoides* L.), and (near the sea) the Acadian savine. Upon comparing what we observe upon our barren lands with the productions of similar soils in Europe, we shall find reason to believe that the heaths and downs of the old country have formerly been forests; and that they might again be covered with wood by imitating the process by which the forest is reproduced on our barrens." This would involve planting the margins of the swamps with the trees and other plants native to the forests of the country.

Differentiation of Forest Types

As might be expected, the different types of forest in Nova Scotia were given special notice, particularly in the unpublished MSS, where Smith discusses individually each of the main tree species. The following notes present his main ecological conclusions. The modern Latin name for each species is included.

Larch, hackmatac, or juniper (*Larix laricina*).—Grows naturally in very barren places, either upon very poor, dry, gravel, upon rocks, or in cold mossy swamps. Seldom more than a foot in diameter.

White pine (*Pinus strobus*).—Grows naturally on wet and dry barren soils, found on all rocky barrens (where it is short), and especially beside lakes. This is the tallest tree in the woods, though not so tall as in New Hampshire. A tree of 60 feet in height and 3 feet in diameter is regarded as large. The best pine occurs on sandy soil.

Yellow pine (*Pinus resinosa*).—Grows in similar soil to white pine, but is much scarcer.

Mountain pine (*Pinus banksiana*).—Very scarce, growing short and scrubbed on the tops of high hills of rock.

Hemlock (*Tsuga canadensis*).—Grows most commonly on gravelly soils, poor but better than the soils of pine; more rarely upon clayey soils. This is one of the largest trees, commonly 2-3 feet in diameter and 60-70 feet in height.

Balsam fir (*Abies balsamea*).—Grows in almost every kind of soil, but thrives best in that which is moist and rich. Not a large tree, seldom more than 15 inches in diameter.

White spruce (*Picea glauca*).—Grows on poor gravelly soil. A large tree but not very plentiful.

Red spruce (*Picea rubens*).—Grows in dry gravelly land, neither very fertile nor barren. More plentiful than pine, and taller than any tree but white pine.

Black spruce (*Picea mariana*).—This is probably a variety of the red spruce, occasioned by the difference of the soil [*cf.* Marie-Victorin 1935]. The leaves are a trifle larger than those of red spruce and have a little difference in their taste. It grows in the most barren places, on rocks, in wet mossy swamps, and on very barren land or gravel. The wood is harder than that of red spruce, owing to its slow growth; every softwood being hardest where the grains or years' growths join, and this hard part being of nearly the same thickness whether the grain be thick or thin. The roots of both red and black spruce spread horizontally, covered only by the turf and moss which always occur on spruce land.

Black or yellow birch (*Betula lutea*).—This tree is considered distinct from the black birch of New York [Smith probably refers to *Betula lenta*], perhaps on account of climatic differences. It is almost always to be found on good land, and often on poor soil; and is said to enrich the soil where it grows. Where the soil is poor it sends out horizontal roots for as much as 50-60 feet. It is a large tree, often 3 feet in diameter.

White birch (*Betula populifolia* and *B. papyrifera*).—This tree is noted as the main species on woodland recently burnt out, provided the soil is not extremely barren.

Dwarf birch (*Betula pumila* or possibly *B. Michauxii*).—This is remarked as a small shrub growing on mossy bogs. While the above two species are not recorded from the mainland of Nova Scotia by Roland (1947), they are given by Fernald (1950), and the habitat note fits best to these plants.

Beech (*Fagus grandifolia*).—Forms the greater part of the woods on the best land, hardwood land being generally covered by beech with a small proportion of birch and maple.

Sugar or rock maple (*Acer saccharum*).—Grows chiefly in moist habitats, near brooks and upon intervals. Always on rich soils, frequent on limestone, and abundant mostly in the eastern part of the province. It is usually from 2 to 3 feet in diameter when mature.

Red, flowering, white, soft maple (*Acer rubrum* and *A. saccharinum*).—Grows on almost all soil types, but best near the water.

Moose-wood maple (*Acer pensylvanicum*).—A small tree, rarely more than 4 inches in diameter, and of very rapid growth. It forms the

principal winter food of the moose except on very barren land where it seldom grows. Chief habitat along small brooks in stony hemlock land.

Dwarf maple (*Acer spicatum*).—A troublesome bush on newly cleared land because of its rapid growth, but only about half the size of the preceding species.

Elm (*Ulmus americana*).—A very rare tree except on the intervals of the eastern districts, where it often grows to 3-4 feet in diameter. It is said that elm ashes contain more than four times as much potash as those of beech or maple.

Horn-beam (*Ostrya virginiana*).—Grows only on rich soils, especially in intervals. It seldom reaches a large size.

Black or pigeon cherry (*Prunus serotina*).—A very rare plant except upon intervals, seldom more than 16 inches in diameter although it grows bigger in the United States.

Red cherry (*Prunus pensylvanica*).—Commonly grows on dry stony ground after burning, but seldom to a size more than 16 inches in diameter.

Choak cherry (*Prunus virginiana*).—A common bush, less than 2 inches in diameter, by brooksides on rich moist upland.

White cedar (*Thuja occidentalis*).—Grows only in the valley of the Annapolis River, and not plentiful there. Smith notes that it is not the same tree as the white cedar of the southern States.

Trembling and white poplar (*Populus tremuloides* and *P. grandidentata*).—These species always grow on burnt land, along with white birch. They are tall but seldom more than 16 inches in diameter.

Mountain ash or Fowlers service (*Sorbus americana*).—A small tree, rarely 6 inches in diameter, growing mostly on very poor soils. The bark is the favorite food of the beaver. The branches are said to be frequently covered with insect nests, even 20 miles from any settlement.

Wild or Indian pear (*Amelanchier*).—A small flowering tree, less than 6 inches in diameter, growing mainly near water on barren soils. Bears good fruit about the size of cherries.

Oak (*Quercus rubra*).—Grows chiefly on poor land, best upon very sandy intervals. It occurs scattered over the province, but reaches a greater size in the eastern parts.

White ash (*Fraxinus americana*).—A very tall tree, usually on rich land and beside brooks, but occasionally in cold swamps.

Black ash (*Fraxinus nigra*).—Grows only in swamps, which, though rich, require draining to produce grass. Seldom of sufficient size to make barrel staves.

With regard to forest communities, Smith remarks that the hardwoods, dominated by beech, occur mainly on the hills, where also the best soils are found. His explanation is that the frequent fires in the lowlands allow nutritive products of organic decay to escape into the air, whence they are blown to the hilltops where the hardwoods absorb them. Probably the burning did have an effect through keeping the communities at an early stage of seral development; and of course the impeded drainage of the lowland causes much of it to be covered with spruce and larch bog, in this heavily glaciated province.

The importance of soil fertility is strongly emphasized in the paper of 1835: "Upon the fertile soils the vegetation is composed of hardwood, and succulent plants with annual leaves. Their growth is rapid, and the outer bark is extremely thin.

Upon a barren soil the trees are evergreen, except the hacmetac: the greater part of the shrubs and plants are also evergreens. Their leaves contain more resinous and more woody matter, than the plants of fertile soils; they have also a strong thick epidermis. The trees on this soil grow slowly, the unusual quantity of epidermis increases in an inverse proportion to the growth of the tree."

In the MSS, Smith has some interesting remarks upon the soils of Nova Scotia. The most fertile soils, occurring beneath hardwoods, are said to be dark in color. On limestone, they are stated to be especially good, and chocolate-colored. In contrast, on the poorest softwood hills the soils were often almost white; undoubtedly Smith was observing the A_2 horizons of podzols. Loams developed from decayed slate were found to be extremely infertile wherever sulphureous iron pyrites was abundant, otherwise this rock did not yield barren soils. Those derived from the granites around Shelburne were claimed to be rather less fertile than usual, a fact associated by Smith with an abundance of isinglass (mica) in them.

Also noted in 1835 was the fact that elm and black cherry, common southward, are restricted in Nova Scotia chiefly to interval soils of an alluvial type. In this connection, it is also of interest that Smith records near Lake Rossignol a number of plants which he knows nowhere else in the province but which grow in the southern States. While he gives no names, it is tempting to see this as the first recognition of the southern coastal plain element in the Nova Scotian flora, especially as green briar (*Smilax rotundifolia*, badly transcribed as *Simula*) and evergreen gallberry (*Ilex glabra*, given as *Prinus Glaber*) occur in his plant lists, with one or two other plants of similar affinities.

The value of ground herbs as indicating soil

type is clearly stated in the MSS, where for example Smith writes of blackberries, virgin's bower and touch-me-not (*Rubus, Clematis,* and *Impatiens*) as plants of rich land suitable for growing timothy grass.

Differentiation of Humus Layers

A most interesting feature of Smith's work is the attention given to humus layers in the forest. In the MSS, soils are said to vary greatly in fertility according to the different proportions and qualities of vegetable mould in them. In the published paper he writes concerning hardwoods: "The annual crop of leaves, the trees overthrown or dying of age, and the lowest twigs, furnish a large quantity of dead vegetable matter, which, by the operations of the Fungi, insects, and the succeeding process of putrefaction, is soon changed into mould, which must continue to accumulate till the trees are fully grown; thus removing to the surface the most fertile part, from the greatest depth to which the roots of a tree can reach. Upon this soil neither turf nor peat earth is formed; but a fine mould lies under the dead leaves." In the case of the evergreens: "The large proportion of two almost imperishable substances, resin, and the epidermis of trees and other vegetables, appears to be connected with the formation of turf; as it is certain that they are produced in the greatest abundance on the most barren soils, and that in the same situations the greatest quantity of turf is formed. It may also be remarked that there are, in the vegetables of the most barren soils, very large proportions of tannin and gallic acid, well known to be very powerful in resisting putrefaction."

After remarking the importance of the moss layer to turf formation (as noted previously), Smith goes on: "Enough, perhaps, has been said of the causes which prevent the rapid change of dead vegetable matter to mould upon barren soils. At any rate a turf *is* formed, the depth of which, in an old forest, is generally in direct proportion to the barrenness of the subsoil. It produces timber fit for many purposes upon the barren whinstone plains, where the surface is covered by from 1 ft. to 2 ft. of broken stone and upon hills of granite which have not 4 in. of soil. It also increases the earthy portion of the turf by slowly decomposing the surface of the subjacent rock.

This turf appears to contain considerable decayed wood, little changed from the state to which it was reduced by the Fungi, and of the epidermis of trees and shrubs, and the cones of spruce very little altered. At the bottom, a very shallow layer, generally mixed with charcoal, approaches to the state of mould. In this bottom layer, the seeds of the raspberry are to be found in abundance, with some of the wild cherry, red-berried elder (*Sambucus pubens* Mx.), and other shrubs that usually spring up after a fire." This ties in with the account of turf activation quoted earlier.

Concluding Remarks

The accuracy of many of Smith's descriptions may be checked by reference to Nichols (1918), who made a study of northern Cape Breton Island in which, for example, the successional role of balsam fir is described, and also the pioneer activity of *Chamaedaphne* (= *Andromeda*) *calyculata* in mat formation around pools. The autecological notes on forest trees compare well with those of Roland (1947). The role of *Baeomyces roseus* in colonizing frost-heaved areas of barren soil has often been observed by the present writer in the vicinity of Halifax, N.S., where also occurs the succession to *Pinus banksiana* as described. The two types of humus layer named mould and turf by Smith parallel the mull and mor of P. E. Müller (*cf.* Romell 1935a, Heiberg and Chandler 1941), and the mould and upland peat of Coville (1913), whose contribution to the study of American forest humus layers is usually overlooked. Incidentally, the last-named writer is perhaps the first to point out the local importance of myriapods as mull-formers. (*cf.* Romell 1935b). While Smith did make mistakes, notably in the assumption that turf is poorly aerated, many others have also fallen into this error, and the excellence of this account of turf activation more than makes up for it.

All in all, it may fairly be claimed that these quotations from Smith's work betray an insight into the pattern and process of vegetation development far in advance of his time. As a fellow ecologist and Nova Scotian, who has lived for many years only a few miles from Smith's home, the present writer is pleased to make this tribute to his memory.

For those interested in the life of this great naturalist, a short biography has been prepared by Piers (1938).

Summary

Attention is drawn to the early ecological studies of Titus Smith, Jr. (1768-1850), whose brilliant observations upon the vegetation of Nova Scotia may well comprise the first major contribution to plant ecology in North America.

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Appendix

Trees and other plants mentioned by Smith, with their probable modern Latin equivalents (nomenclature according to Fernald 1950).

Smith's common name	Smith's Latin name	Modern Latin equivalent
	Trees (in the order of autecological notes in text):	
Larch, Hackmatack or Juniper	*Pinus Larix*	*Larix laricina* (Du Roi) K. Koch.
White Pine	*Pinus Strobus*	*Pinus strobus* L.
Yellow Pine	*Pinus Sylvestria*	*Pinus resinosa* Ait.
Hudson's Bay Pine, Mountain Pine	*Pinus Banksiana* Lamb., *Pinus Pinea*	*Pinus banksiana* Lamb.
Hemlock	*Pinus, Abies canadensis* Mx.	*Tsuga canadensis* (L.) Carr.
Balsam Tar or Fir	*Pinus balsamifera, Abies balsamifera* Mx.	*Abies balsamea* (L.) Mill.
White Spruce	*Pinus*	*Picea glauca* (Moench) Voss
Red Spruce	*Pinus*	*Picea rubens* Sarg.
Black Spruce	*Pinus*	*Picea mariana* (Mill.) BSP.
Black or Yellow Birch	*Bitula nigra, Betula excelsa* H.K.	*Betula lutea* Michx. f.
Black Birch of New York	———	*Betula lenta* L.?
White Birch	*Bitula alba, Betula populifolia* H.K.	*Betula papyrifera* Marsh., *B. populifolia* Marsh.
Dwarf Birch	*Bitula nana*	*Betula pumila* L. or *B. michauxii* Spach
Beech	*Fagus sylvatica* L., *Fagus ferruginea* L.	*Fagus grandifolia* Ehrh.
Sugar, Rock, Curled or Birdseye Maple	*Acer Saccharinum*	*Acer saccharum* Marsh.
Red, Flowering, White or Soft Maple	*Acer rubrum, Acer dasycarpon* Ehrh., *Acer eriocarpon* Mx.	*Acer rubrum* L., *A. saccharinum* L.
Moosewood Maple	*Acer*	*Acer pensylvanicum* L.
Dwarf Maple	*Acer Mana*	*Acer spicatum* Lam.
Elm	*Ulmus Americana*	*Ulmus americana* L.
Hornbeam	*Carpinus Ostria*	*Ostrya virginiana* (Mill.) K. Koch.
Black or Pigeon Cherry	*Prunus*	*Prunus serotina* Ehrh.
Bird or Red Cherry	*Prunus Avisim*	*Prunus pensylvanica* L. f.
Choak Cherry	*Prunus Virginica*	*Prunus virginiana* L.
White Cedar	*Thaya Occidentala*	*Thuja occidentalis* L.
Trembling Poplar	*Populus Tremula*	*Populus tremuloides* Michx.
White Poplar	*Populus Alba*	*Populus grandidentata* Michx.
Mountain Ash or Fowler's Service	*Sorbus Aucuparia*	*Pyrus americana* (Marsh.) DC.
Wild or Indian Pear	*Mespilus*	*Amelanchier* Medic.
Oak	*Quercus rubra*	*Quercus rubra* L.
White Ash	*Fraxinus Americana*	*Fraxinus americana* L.
Black Ash	*Fraxinus*	*Fraxinus nigra* Marsh.

Other plants (roughly in order of appearance in text):

Kalmia, Dwarf Laurel	*Kalmia*	*Kalmia angustifolia* L.
Raspberry	*Rubus Idaeus*	*Rubus idaeus* L.
Red-berried Elder	*Sambucus racemosa, Sambucus pubens* Mx.	*Sambucus pubens* Michx.
Sumach	*Rhus conidensis*	*Rhus typhina* L.
Prickly Aralia or Sarsaparilla	*?Aralia spinosa*	*Aralia hispida* Vent.
Evergreen fumitory	———	*Corydalis sempervirens* (L.) Pers.
French Willow	*Epilobium angustifolium*	*Epilobium angustifolium* L.
Cacalias	———	Compositae (see Lindley and Moore 1870) inclusive term
Blueberry	*Vaccinium Album, ?Vaccinium ?venustum* H.K.	*Vaccinium* L.
Brakes	———	*Pteridium aquilinum* (L.) Kuhn, and other ferns?
Sweet Fern	*Myrica Asplinifolio, Comptonia aspleniifolia* H.K.	*Comptonia peregrina* (L.) Coult.
Dwarf Willows	*Salix*	*Salix* L.
Withrod	*Viburnum*	*Viburnum cassinoides* L.
Alder	*Bitula Alnus*	*Alnus crispa* (Ait.) Pursh and *A. rugosa* (Du Roi) Spreng.
Rhodora	*Rhodora Canadensis* L.	*Rhododendron canadense* (L.) Torr.
Mayflower	*Ehigola*	*Epigaea repens* L.
Trailing evergreens	*Lycopodium* species	*Lycopodium* L.
Snakeroot	*Aristolochia Serpentaria* L.	Not present in N.S., the writer is at a loss for the correct plant
Mitchella	*Mitchella repens* W.	*Mitchella repens* L.
Linnea	*Linnaea borealis* Gron.	*Linnaea borealis* L.
Pigeonberry	*Cornus Canadensis*	*Cornus canadensis* L.
Mountain tea	*Gaultheria procumbens* L.	*Gaultheria procumbens* L.
Maidenhair	*Vaccinium Hispidulum, Adiantum pedatum* in error in 1835	*Gaultheria hispidula* (L.) Bigel.
Aster	*Aster,* several nondescript species	*Aster* L.
Goldenrods	*Solidago,* several species	*Solidago* L.
———	*Lichen ericetorum*	*Baeomyces roseus* L.
Caribou (reindeer) moss	———	*Cladonia rangiferina* L.
Hawkweed	*Hieracium*	*Hieracium* L.
Acadian heath	*Ceratiola ericoides* L.	*Corema Conradii* Torr.
———	*Potentilla tridentata*	*Potentilla tridentata* Ait.
Black Whortle	*Vaccinium Myrtillus*	*Vaccinium* L.
Candleberry Myrtle	*Myrica cerifera*	*Myrica pensylvanica* Loisel.
Round-leaved Andromeda	*Andromeda calyculata*	*Chamaedaphne calyculata* (L.) Moench
Bog Moss	———	Presumably *Sphagnum*
Indian Cups	*Sarracena purpurca*	*Sarracenia purpurea* L.
Indian Tea	*Ledum*	*Ledum groenlandicum* Oeder
Rosemary-leaved Kalmia	*Kalmia glauca* L. var. *rosmarinifolia* Ph.	*Kalmia polifolia* Wang. or possibly *Andromeda glaucophylla* Link
Dutch Myrtle	*Myrica Gala*	*Myrica gale* L.
Cotton Grasses	*Eriophorum Alpinum*	*Eriophorum* L.
Sedges	*Carex,* several species	*Carex* L.
Bearberry, Uva-ursi	*Arbutus Alva Ursc*	*Arctostaphylos uva-ursi* (L.) Spreng.
Berry-bearing Heath, Crakeberry Heath	*Empetrum nigrum* L.	*Empetrum nigrum* L.
Yellow-flowering cistus	*Hudsonia ericoides* L.	*Hudsonia ericoides* L.
Acadian savine	*Juniperus Sabina*	*Juniperus horizontalis* Moench
Green Briar	*Simula rotundifolia*	*Smilax rotundifolia* L.
Evergreen Gall berry	*Prinus Glaber*	*Ilex glabra* (L.) Gray
Blackberry	*Rubus Fructicosus*	*Rubus* L., Subgenus *Eubatus* Focke
Virgin's bower	*Clematis vitalla*	*Clematis virginiana* L.
Touch-me-not	———	*Impatiens* L.

N.B. In the MSS, Smith's Latin names were often badly transcribed from the original document, witness for example *Ehigola* for *Epigaea*. Those of Smith's Latin names with authorities come from the published paper, as do a few of those without.

SUBALPINE FUNGI AND SNOWBANKS

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Introduction

The study of the environment, especially the microenvironment, of the macromycetes (larger fungi) of the soil has received little attention. Persons describing the fungi of a region, or writing descriptions of new or interesting species of fungi, indicate something of the habitat but nothing of the actual conditions under which the fungus in question was growing. The present notes were prepared as a result of several seasons of field observations. They are presented in their present imperfect form in the hope that some student of biotic relationships may be interested in the problems involved and have the time and opportunity to subject them to further study.

Historical

Setchell and Watson (1926) attempted to correlate some of the climatic conditions they found at the soil surface with the occurrence of hypogaeous fungi (fungi which fruit underground) at a station in the Santa Cruz Mountains south of San Francisco, California. The study was very limited and of doubtful value, attempting to indicate some relationship between the occurrence of fruit-bodies and the three-day fogs reportedly characteristic of the region, but describing none of the actual soil conditions nor of the conditions giving rise to the fogs. Weir (1918) listed the wood decay fungi of northern Idaho and adjacent Montana, and Washington according to host range and highest altitude at which they had been collected. No further correlation was attempted. In the literature of phytopathology (Foister 1935, 1946) there is a large number of references to climatic factors in reference to plant disease fungi.

At high altitudes, however, few fungi are reported to be of economic importance. Those which are of some importance include species in the genera *Herpotrichia* and *Neopeckia,* smothering fungi of coniferous trees (Hedgcock 1914). In forest nurseries at high altitudes certain soil fungi (micromycetes) are also of importance, especially in the genus *Pythium* and physiologically related organisms which cause damping-off disease of seedlings (Baxter 1943). Both of these groups of fungi appear to require high relative humidities. The smothering fungi appear to develop only under the influence of the winter snowpack, the damping-off fungi develop only in moist soil. Both habitats are ones in which nearly, if not actually, 100 per cent relative humidity occurs.

Several collectors have reported on fungi collected at high altitudes and latitudes. Lind (1934) obtained from collections of vascular plants housed in Scandinavian herbaria a series of species of micromycetes to which the vascular plants were host in either living or dead tissues. He made several reports on these but no attempt was made to correlate the collections with climatic or edaphic factors beyond the assumptions inferred when the areas reported were listed as north of the Arctic Circle. Wehmeyer in Wyoming (1946, 1947) and Cooke (1944) on Mount Shasta, California, have reported on collections of fungi but no correlation other than host, specific location, or Merriam life-zone was attempted by either worker. Many collectors have published descriptions of macromycetes collected in the high mountains of western North America; many papers have been written on the species, but little or no information has been obtained as to the micro-environments of the various species discussed.

Following a severe drought, Shope (1936) reported that the fungi associated with spruce in subalpine habitats in the Colorado Rocky Mts. were killed out in spite of the fact that some could have been mycorrhizal and that observations were made over a very limited period of time by qualitative rather than quantitative methods. Shope (1937) indicated that revival of the populations was more rapid in soilborne fleshy species than in wood-borne species producing leathery or woody fruit bodies. Following the same period of drought, on the other hand, Martin (1937) found that fungi growing in the soil in Iowa revived and fruited after an interval which was somewhat longer than usual. Revival in Iowa appeared to have been correlated with moisture made available by precipitation. Again the report was based on observation of qualitative rather than quantitative data. Friedrich (1940) published data to show that certain species of agarics (mushrooms) can fruit at any elevation in the Austrian Alps, while others are restricted to certain elevations. Some species have a maximum altitude above which they are not found. Some are equally at home near a glacier at high altitudes or in a farm yard at rela-

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tively low altitudes near Vienna. These points were emphasized in a survey of fungus populations in the Otztaler Alps (Friedrich 1942).

During the eight summers spent by the writer on Mount Shasta in northern California, it was observed that around snowbanks special groups of macromycetes occurred. The first realization of the possible relationship between snowbanks and fungi came as the result of the observation of fruit bodies of *Polyporus alboluteus* and *Polyporus leucospongia*. In the case of the former, the fruit bodies appeared to have been developed before the snowpack melted for they were in fresh condition upon being exposed to the air. Within two weeks, most fruit bodies were piles of red dust under the logs on which they grew, having been eaten by small beetles (*Dacne picea*). The fruit bodies of the second species dried up soon after the snow melted and were found again in fresh condition only after infrequent showers. Eventually it was observed that other fungi were associated almost exclusively with snowbanks. A gray species of *Lyophyllum*, as yet unidentified, and *Tricholoma rhizoideum*, were found commonly around melting snowbanks. *Paxina nigrella* grew only near snowbanks in the process of melting and in one year, following a very heavy snowpack, it was found to occur at the edge of a snowbank week after week for at least four weeks as the snow receded. Over twenty specimens were found in fresh condition within a foot of the snowbank on each of four weekly visits. Away from the influence of water from melting snow, and the higher humidity near the melting snowbank, all specimens were dry. *Mycena griseoviride* and *Hygrophorus vernalis*, first reported by A. H. Smith from specimens collected near snowbanks in the Olympic Mountains, grew near snow and even up through snow at the edge of the pack from very rotten logs of Shasta fir (*Abies magnifica* var. *shastensis*) or from soil. *Secotium nubigenum* grew on decaying twigs, branches and logs of Shasta fir near or under snowbanks. Squirrels like to eat the fruiting bodies of this species and where it occurs away from snow in fresh or dry condition, they may show marks of having been tasted by them. Specimens have been found set out to dry on stones, branches of young trees, and in sunny places, apparently for later storage and subsequent use as food.

Similar series of species of fungi have been observed by the writer on Lassen Butte, California; Crater Lake, Santiam Pass, Williamette Pass, MacKenzie Pass and Mt. Hood, Oregon; Mt. Adams, Mt. Rainier and Mt. Baker, Washington; the Blue Mountains in northeastern Oregon, the Wasatch Mountains in Utah, and the Medicine Bow Mountains in Wyoming. From reports of collections, a more or less similar series also occurs in the Sierra Nevada of California, especially at Tioga Pass, and in the Olympic Mountains in northwestern Washington.

Climatologic Data

An estimate of the meterologic data for the macroenvironments of habitats in subalpine and timberline areas must be obtained by the observer in most cases. The 1946 meteorologic summaries show the inadequacies of standard Weather Bureau data for a study of climatic conditions at timberline on mountains in California, Oregon and Washington. The nearest Weather Bureau stations to habitats sampled lie in California at the base of Mount Shasta in the Sierra mixed conifer zone; in Oregon in the upper *Abies-Tsuga* zone or at timberline; and in Washington in the lower *Tsuga-Thuja* zone, the upper *Tsuga-Thuja* zone and in the *Abies-Tsuga* zone. Few, if any, published timberline data for year-round precipitation and temperature are available for Mt. Shasta, Mt. Adams, Mt. St. Helens, Mt. Rainier, or Mt. Baker. The habitats which have been studied here, and which are described below, lie in the upper *Abies-Tsuga* zone or higher.

The cooperative snow surveys maintained by the western states in connection with various private, state and federal agencies report monthly during the winter and early spring the status of the snow crop as to date of survey, depth of snowpack, density and water content of snow, both as to its present status and in comparison with the averages of the previous yearly surveys. On the basis of such surveys, an approximation of spring run-off in relation to floods and water available for irrigation is forecast. Such data have been obtained for areas near most of the sampling stations described below and the data for the deepest recorded pack for the season for the years in which the areas were visited are presented in the habitat descriptions in the following section of the paper.

At Mount Shasta, there is little precipitation between the melting of the snowpack of one season and the formation of the pack in the following season. Here the data for the deepest pack give a fair approximation of the total precipitation for the year. This is borne out by data obtained by the totalizer which, despite efforts to prevent loss by evaporation, records less precipitation than the water content recorded for the deepest snowpack. Other areas, subject to heavier summer and fall precipitation, require greater dependence on total-

izer data or on data recorded by more adequate instrumentation.

Descriptions of Habitats

California

Lassen Butte.—Lassen Volcanic National Park. Above King Creek Meadows near California State Route 89, 7500-8000 feet. *Abies magnifica* var. *shastensis—Tsuga mertensiana* association, *Abies-Tsuga* zone. July 1, 1950. Slope gentle. Andesitic lava stones, pebbles and sand covered with a relatively thin layer of duff and litter. Southeast-facing.

Mount Shasta.—Shasta National Forest, Siskiyou Co., Panther Creek Meadows.

On May 4, 1948, snow depth at Sand Flats, 7000 ft., was 106.2 inches, water content 38.0 inches. At 8000 ft., Horse Camp, snow depth 131.1 inches, water content: 59.2 inches.

On March 17, 1951, snow depth at Sand Flats was 103.6 inches, water content 39.3 inches; at Horse Camp snow depth was 134.1 inches, water content 41.9 inches.

These were the deepest packs recorded for the season but total precipitation was probably somewhat greater than reported water content of snow.

Plot 1. Rocky creek valley on terminal moraine. Spaces between boulders have become filled in with gravel which is covered with a thin layer of duff and litter. Parent material andesite. *Abies magnifica* var. *shastensis—Tsuga mertensiana* association, *Abies-Tsuga* zone. Shrub layer composed of *Phyllodoce empetriformis, Vaccinium caespitosum,* and *Kalmia latifolia.* Nearly level. July 4, 1948. 7600 ft. South-facing.

Plot 2. Nearly level gravelly bench on a low lava ridge. *Abies magnifica* var. *shastensis* association, *Abies-Tsuga* zone. No shrubs, thin layer of duff and litter on fine gravel. July 5, 1948. South-facing. 7600 ft.

Plot 3. East side of Grey Butte Pass east of Panther Creek Meadows. Steep mid-slope facing southeast. *Tsuga mertensiana-Abies magnifica* var. *shastensis* association, *Abies-Tsuga* zone. 7600 ft. July 4, 1951.

Plot 4. Near Plot 3, little duff and litter, added factor of the presence of *Phyllodoce empetriformis* and fallen hemlock log. Same date.

Oregon

Crater Lake National Park.—Colonades area, Annie Creek. Forest floor level, with thick duff and litter layers on andesitic sand and gravel. *Tsuga mertensiana* association, *Abies-Tsuga* zone. June 29, 1948. 5000 ft. South slope. The snow survey made at 4500 feet, March 31, 1948, gave a snow depth of 129 inches with a water content of 49.8 inches.

Willamette Pass.—Along Oregon State Route 58, June 8, 1951. 5000 ft. Nearly level. Similar to Santiam Pass plot.

Santiam Pass.—Fairly level area at summit of ridge. Thin layer of litter and duff on fine to coarse andesite gravels. *Picea engelmannii—Tsuga mertensiana—Pinus contorta* var. *latifolia* association, *Abies-Tsuga* zone. July 7, 1948. 5000 ft. The snow survey on March 25, 1948, gave a snowpack of 97.0 inches with a water content of 34.2 inches.

Washington

Mt. Adams.—Between Mirror Lake and Bird Creek Meadows. *Tsuga mertensiana—Abies lasiocarpa* association, *Abies-Tsuga* zone. Thin litter and duff layers on fine to coarse andesitic gravels. Nearly level. 5000 ft. July 9, 1948. South slope.

Mt. Rainier—Mt. Rainier National Park. Southwest slope. Paradise River Valley along road below Paradise Lodge. *Abies lasiocarpa—Tsuga mertensiana* association with low tree layer of *Chamaecyparis nootkatensis* and shrub layer including *Vaccinium, Phyllococe* and *Alnus. Abies-Tsuga* zone. Thin litter and duff layers on fine to coarse granitic gravels. 4800 ft. July 9, 1948. The snow survey at 5000 ft. on Mar. 31, 1951, gave a snow depth of 190 inches with a water content 81.4 inches.

Mt. Rainier.—Mt. Rainier National Park. East slope. First switch-back below Sunrise Point, Yakima Park Road. 5700 feet. July 10, 1948. *Abies lasiocarpa—Tsuga mertensiana—Picea engelmanii* association, with a good herb layer, *Abies-Tsuga* zone. North-facing slope in creek valley. Thick litter and duff layers on granitic materials. The closest snow survey was made at 3000 feet at White River Entrance. On April 3, 1948 the snow depth was 65.0 inches with a water content of 22.9 inches. Although this lies in the "rain shadow" of the mountain, snow depth and water content were probably greater at 5700 feet although not as great as at Paradise Lodge on the west side of the mountain.

Oregon

Blue Mountains.—Horseshoe Prairie, Umatilla National Forest, Union Co., near Oregon State Route 204. Nearly level, south-facing slope. *Abies lasiocarpa—Larix occidentalis—Picea engelmannii* association, *Abies-Tsuga* zone. 5000 ft. June 10, 1949. Thin litter and duff layer on granitic gravels. The snow survey at Tollgate, Sta-

tion 212, on March 29, 1949, gave a snow depth of 99.0 inches with a water content of 44.5 inches.

Blue Mountains.—Near head of Little Phillips Creek. Similar to preceding plot. Same date.

Utah

Wasatch Mountains.—Top ridge above Parrish Creek Experimental Plots, 9200 feet, Davis Co. Gentle slope under small grove of *Abies lasiocarpa* and *Picea engelmannii, Abies-Tsuga* zone. In an open fell-field. Thin litter and duff layer on granitic gravels. Grove isolated in an area dominated by *Artemisia* and other shrubs. Southeast-facing. June 20, 1950. The nearest snow survey station in 1950 was that at Barnard Creek where at 9000 feet on April 2 the snow depth was 75.9 inches with a water content of 30.3 inches.

Wyoming

Medicine Bow Mountains.—Vicinity of Tanner Lake, three miles above University of Wyoming Summer Science Camp, Albany Co., 10,000 feet. Aug. 20, 1950. Gentle south-facing slope. *Abies lasiocarpa-Picea engelmannii* association.

Such devious methods for obtaiinng climatic data only indicate that a supply of water is held in snow for a certain period of time on the ground surface. As the pack begins to melt, water is lost by evaporation and basal melting. Basal melting and melting near metabolizing organisms make water available to any organism which requires it. These organisms are then able to utilize the water and develop at low temperatures as the water is released from the snowpack.

Microclimatic data such as rate of snow-melt, local intermittent precipitation, air temperature, relative humidity and soil moisture must be obtained on the spot by the observer over a longer period of time than may seem to be required for the observation of the desired organisms.

Experimental

A trip to the Blue Mountains of northeastern Oregon in the early summer of 1948 pointed up a comparison between the fungi of snowbanks in that region and of Mount Shasta. It was thought that other areas might have a similar mycobiota and prior to a trip to the Cascade Mountains for polypore collecting, R. Daubenmire suggested a method for studying these habitats. Plots, 3 x 8 dm. in size, were set up in series from within the snowbank to the dry area beyond it. In the center of each plot a thermometer was inserted 1 dm. into the soil. After equilibrium had been reached the temperature of the soil was obtained by reading the thermometer as quickly as possible after removing it from the soil. Later a series of thermometers was placed along the edge of the snowbank. In the first series, no reading under zero degrees centigrade was obtained, and as one neared the edge of the snowbank and proceeded outward the temperature increased. In the second series, readings were approximately the same along the edge of the snowbank and similar to readings from comparable sites in the first series. The species of fungi and the location of their fruit bodies were recorded and mapped for each set of plots studied. Specimens of most species of the fungi collected in California were deposited in the herbarium of the University of California, Berkeley; material of most species from other states was deposited in the herbarium of the Department of Plant Pathology, The State College of Washington, Pullman.

Results

Snowbank fungi have been observed at stations from Lassen Butte to Mount Baker in the Cascade Mountains, and eastward in the Blue Mountains, the Wasatch Mountains and the Medicine Bow Mountains. For each of eight series of plots temperature of the soil at 1 dm. together with the date, time of observation and general weather conditions are presented in Table I. For ten sets of plots studied, Figure 1 gives the location of snowbank, fungus fruit bodies, and position of the stab thermometers. In the twelve mountain areas studied, certain fungi are common. Fifteen of these species are tabulated (Table II) indicating in which area each species was found at the time of observation. These fungi are present in other areas which were not included in this study. One species restricted to a host is included since it is seen only during the melting of snowbanks; it is almost invisible when dry. Species present in the area but not immediately adjacent to the snowbanks at the time of observation are noted.

These species are listed by location regardless of the year in which the observations were made for, to greater or less extent, the same species appear year after year as the snow recedes. Numbers of fruit bodies shown on the charts in and near the plots are not necessarily indicative of the abundance of the species for in some cases many more fruit bodies occurred in the area. In most cases, plots were set up where it was convenient to measure temperature at one dm.

Discussion

The soil in most of the areas observed is covered by a layer of duff overlain by a layer of litter, both of which are consolidated into a rather thick mat which may become cracked as it dries out.

TABLE I. *Soil temperatures in ° C. at 1 dm. depth*

Weather....	Sunny	Sunny	Sunny	Low fog, clouds, rain	Overcast	Overcast	Sunny	Sunny
Date.....	6-29-48	7-4-48	7-4-48	7-5-48	7-7-48	7-9-48	6-10-49	7-4-51
Figure.....	1	2	3	4	5	6	7 & 8	9 & 10
Location...	Santiam Pass 1:00 P.M.	Mt. Shasta 10:30 A.M.	Mt. Shasta 11:45 A.M.	Crater Lake 8:15 A.M.	Mt. Adams 1:45 P.M.	Mt. Rainier 6:00 P.M.	Blue Mts. 11:00 A.M.	Mt. Shasta 5:40 P.M.
Plot								
1.....	1.0	0.25	0.5	0.25	0.5	1.0	0.2	—
2.....	1.5	0.5	1.0	0.5	1.5	1.25	1.0	1.8
3.....	6.0	1.5	3.0	2.0	3.0	2.5	3.0	—
4.....	9.0	1.0	4.0	4.0	4.2	4.0	3.2	5.5
5.....	—	2.0	4.5	4.5	4.25	5.5	4.0	6.0
6.....	—	3.0	5.0	5.0	4.75	5.75	5.1	—
7.....	—	—	—	—	—	—	5.0	—

Snow line approximately in middle of second plot in each case.

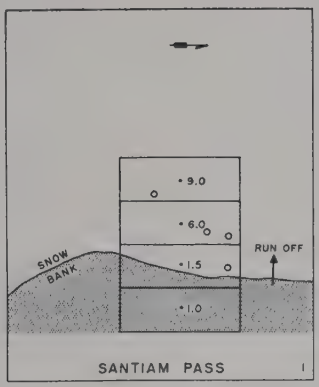
TABLE II. *Observed distribution of common subalpine fungi*

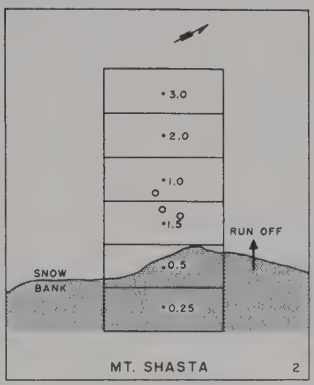
Locations.....	California		Oregon				Washington				Utah	Wyoming
								Mount Rainier				
Fungi	Lassen Butte	Mount Shasta	Crater Lake	Willamette MacKenzie Santiam Passes	Mount Hood	Blue Mts.	Mount Adams	W	E	Mount Baker	Wasatch Mts.	Medicine Bow Mts.
Arthrinium cuspidatum (Cke. & Harkn.) v. Hoehn.	*	*	..	..	..	..	..	..	..	*	..	*
Calvatia fumosa Zeller	..	*	*	*	*	..	*	*	*	..	..	*
Dasyschpha arida (Phil.) Sacc.	*	*	*	*	*	*	*	*	*	*	*	*
								*	..	..	..	
Gelatinodiscus flavida‡ Kanouse	..	..	..	..	..	..	..	*	..	..	..	
Guepiniopsis alpinus (Tr. & Earle) Brasfield	*	*	*	*	*	*	*	*	..	*	*	*
Hygrophorus vernalis A. H. Smith	..	*	*	..	..	..	*	..	*	..	..	.
Lentinus sp.	..	*	*	..	..	*	*	*	*	..	*	.
Lyophyllum sp.	*	*	..	*	..	*	*	*	*	..	*	.
Metasphaeria sepalorum Vleugel	*	*	..	..	..	..	*	..	*	*	.	.
Mycena griseoviride A. H. Smith	..	*	..	*	..	*	*	..	..	..	.	.
Pazina nigrella Seaver	*	*	..	..	..	*	..	*	*	..	..	..
Polyporus alboluteus Ell. & Ev.	*	*	*	..	*	*	†	..	..	..	..	*
Polyporus leucospongia Cke. & Harkn.	*	*	*	*	*	*	*	*	*	..	*	*
Secotium nubigenum Harkn.	*	*	*	*	..	..	*	..	..	..	..	..
Stereum rugisporum (Ell. & Ev.) Burt.	*	*	*	*	*	*	*	†	..	*	..	*

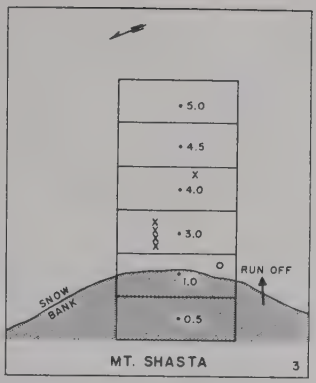
*Present in plot area at time of visit.
†Present in area but not in immediate vicinity of plots.
‡Associated only with *Chamaecyparis nootkatensis* (D. Don) Spach and observed only in snow-banks.

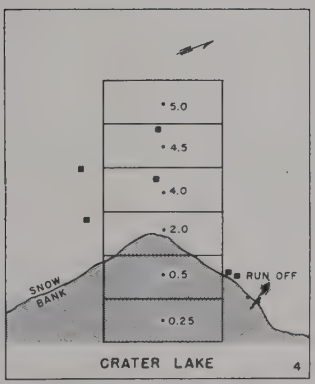
Beneath this mat is humus-bearing mineral soil which is very sandy and gravelly. Usually the soil is very shallow and much parent material is included in the top decimeter or two in the form of large pebbles, boulders, rock outcroppings, etc. In the lower part of the first decimeter, occassionally a gray layer is found which may be rather shallow. The water from the melting snow irrigates the soil within a few decimeters of the snowbank beyond which the soil dries out rapidly because of the high porosity producing rapid percolation or because of the relatively low surface air humidities. The soil wilting percentage for the fleshy fungus fruit bodies (mushrooms) appears to be very high here; in fact it appears to be much higher than that of the green plants which occur in the area. This factor appears not to have been studied in the field in relation to the fruiting of fleshy fungi. There are papers based on laboratory observations which discuss the temperature of and evaporation from both the upper surface and the greatly enlarged gill surface of fungus fruit bodies (Friedrich 1940). The fact that fungus fruit bodies dry out relatively near a source of water supply indicates that in addition to the requirement of the fungus mycelium for a high relative humidity in the soil, the fruit body itself requires a high relative humidity in the surface layers of air in which it develops, produces and discharges its spores. It may also indicate that the mycelia of these fungi inhabit mainly the superficial layers of the soil which become dried out quickly.

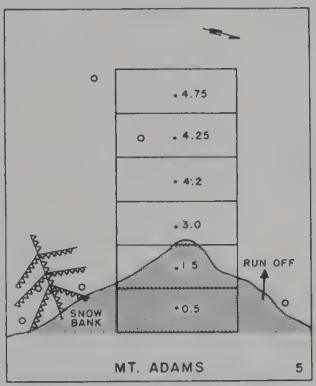
To study these phenomena of moisture relationships, including soil moisture, soil humidity and surface air humidity, and the relationships between the fungi and these phenomena and their habitat, certain data are required which cannot be obtained by existing techniques. In completely saturated soil, the fungus probably could not

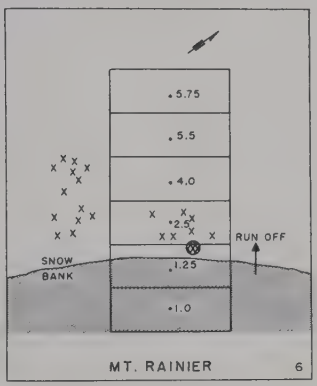


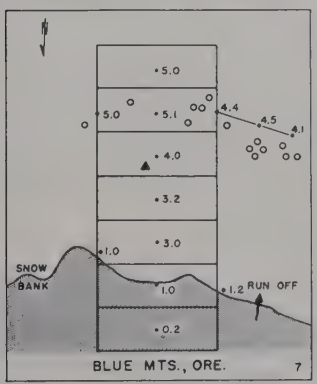


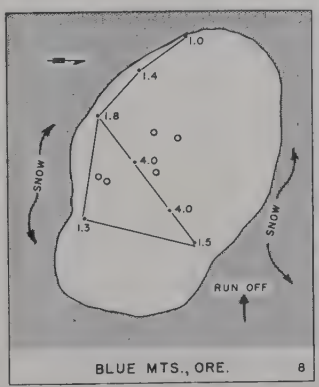


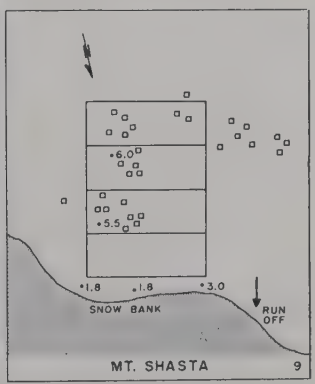


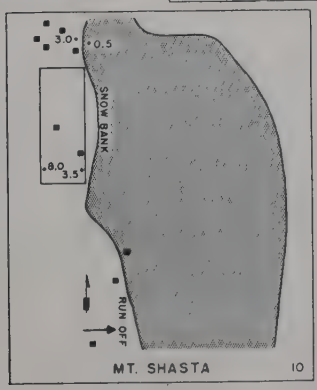












LEGEND

- o LYOPHYLLUM SP.
- ■ HYGROPHORUS VERNALIS
- ▲ OTIDEA FULGENS
- ⊗ CANTHARELLUS CIBARIUS (GROUP FROM PREVIOUS FALL)
- X PAXINA NIGRELLA
- ΔΔΔ DASYSCYPHA ARIDA
- □ MYCENA GRISEOVIRIDE
- •1.0 – DEGREE C. AT 1 DM

DIAGRAMS OF PLOTS AT EDGE OF SNOW BANKS SHOW POSITIONS OF THERMOMETERS AND TEMPERATURES RECORDED, NORTH DIRECTION, RUN OFF DIRECTION, AND POSITION AND SPECIES OF FUNGI FRUITING IN AREA.

exist (or if present would be dormant) since it is an aerobic organism and a completely saturated soil would produce anaerobic conditions. Information is needed on the relative amounts of water and air present in the region of growth of the mycelium as indicated by fruit body production both under, next to, and away from the snowbank. Information is needed on the minimum, optimum, and maximum amounts of water and air in a given amount of soil at certain temperatures in relation to the growth and fruit body development of these fungi. Information is needed as to the approximate position of the mycelium in the soil, where it occurs in relation to the organic components, which fraction it utilizes (cellulose, lignin, or other), whether or not it is mycorrhizal, how much humidity is required to keep the fruit bodies turgid for spore discharge (including information on transpiration stress), and data on other factors as yet not determined. The techniques developed by Warcup (1951) for the study of Basidiomycetes in the soil, as well as other techniques could well be applied here.

Summary

A number of species of macromycetes has been found in widely spaced areas throughout the western United States in subalpine habitats. The occurrence of these species in relation to snowbanks is indicated. The climatic data available are presented, in part, and discussed. Pertinent questions to be answered are discussed together with some techniques which can be used to discover answers.

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RADIAL GROWTH IN NINE SPECIES OF TREES IN SOUTHERN LOUISIANA[1]

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Introduction

During recent years, especially since the publication by Reineke (1932) and Daubenmire (1945) of directions for making cheap, rapid, and reasonably accurate dendrometers, there has been increased interest in the subject of tree growth. Numerous papers, reporting on growth of trees in many parts of the United States and Canada, have appeared. The present paper is a report on observations made on tree growth in still another area, southern Louisiana.

The purpose of the study was to determine the magnitude and time of radial increase of trees of several species native to the New Orleans area, to correlate radial increase with leaf development and, as far as possible, with certain environmental conditions.

[1] Support for this work was made available by the Tulane University Council on Research from the Carnegie Foundation Research Fund.

Seventy-three trees located in two areas were selected for measurement. One was injured by vandals and two died from other causes, but records were carried through to completion on 70 trees.

One of the areas was a part of the batture of the Mississippi River, in Jefferson Parish, Louisiana. The batture is the area between the levee and the river. The soil is a coarse silt, and drainage is good except at time of high water. The batture is under water at time of flood stage; however, flooding did not occur during the year this study was made. Trees measured in the batture area were as follows: cottonwood (*Populus deltoides* Bartr.), 13 trees, ranging from 7 to 30 inches diameter; sycamore *Platanus occidentalis* L.), 9 trees, 7½ to 20 inches diameter; black willow (*Salix nigra* Marsh.), 10 trees, 7 to 16½ inches diameter; live oak (*Quercus virginiana* Mill.), 1 tree, 10 inches diameter; hackberry (*Celtis laevigata* Willd.), 9 trees, 8 to 14 inches diameter.

The second area was a cypress-tupelo swamp in St. Charles Parish, Louisiana. All large bald cypress had been cut some time in the past and what remained was second-growth, along with tupelo gum and other species. The soil in this area is clay; drainage is poor. Trees measured were as follows: black willow, 3 trees, 7 to 16 inches diameter; hackberry, 1 tree, 13 inches diameter; bald cypress (*Taxodium distichum* Rich.), 11 trees, 6½ to 16½ inches diameter; tupelo gum (*Nyssa aquatica* Marsh.), 9 trees, 12 to 18 inches diameter; Drummond red maple (*Acer drummondii* Hooker and Arnold), 2 trees, 8 and 11 inches diameter; trident red maple (*Acer rubrum* var. *tridens* Wood.), 2 trees, 8½ and 11½ inches diameter.

Methods

A dendrometer, made according to directions given by Daubenmire (1945), was used. The dial gauge used was an Ames, number 262, which measures to 1/1000 inch. Three, 2 inch, brass screws set through the bark and well into the wood furnished the permanent reference base. A small square of galvanized light weight sheet iron was fastened to the bark with marine glue, in position to contact the dial spindle. All radial measurements were made on the north sides of the trees, at a distance of approximately 4½ feet from the ground. Measurements were made once a week, usually on the same day, from early March, 1951, to August 15, 1951, and then less frequently to March 30, 1952. The dates when measurements were made are indicated in Figures 1 to 3.

Results

Mean total radial increase

The mean total radial increase for trees of each of the nine species, during approximately a year, is presented in graphic form in Figures 1 to 3; see also column 1, Table I. Cottonwood was the fastest growing tree, having a mean radial increase of 0.315 inch for a year. Next in order came sycamore, willow, live oak, hackberry, bald cypress, tupelo gum and last, the two kinds of red maple. Live oak has a local reputation for slow growth and it is interesting to find that it ranks fourth in growth rate in the list of nine species.

Many of the papers which have reported on tree growth fail to report actual radial increase; instead, time is plotted against percentage of total growth attained by each date. The author of this paper believes actual growth is important and should be reported.

Beginning of radial increase

The time when each species started radial increase in the spring and ceased in the fall is given in columns 2 and 3 of Table I. These times were determined from the records for individual trees and may not agree exactly with the record indicated by the curves in Figures 1 to 3 which are based on mean values of all individuals of each species.

Live oak was the first species to begin radial increase; it began on about February 25 in 1951, and also in 1952. During the period from March 10 to 24 a majority of all the trees began to increase in radius. All trees of hackberry, cottonwood, the two kinds of red maple, and the black willows in the cypress-tupelo swamp began to increase during this period. Black willows on the batture did not begin until about 5 weeks later. This difference in time for the black willows is probably due to a difference in air temperature between the two places. Bonck and Penfound (1944) have pointed out that trees on the batture are late in starting growth because of the cooling effect of river water. Sycamore began growth between March 24 and April 6. There was more variation between different individuals of bald cypress and tupelo gum in starting growth than between members of the other species. Start of diameter increase for different bald cypresses varied from March 9 to April 20, and tupelo gum varied between March 15 to June 30.

Cessation of radial increase

Bald cypress was the first species to stop radial increase. Five trees stopped by June 1, two more by July 12, and the other four by July 26.

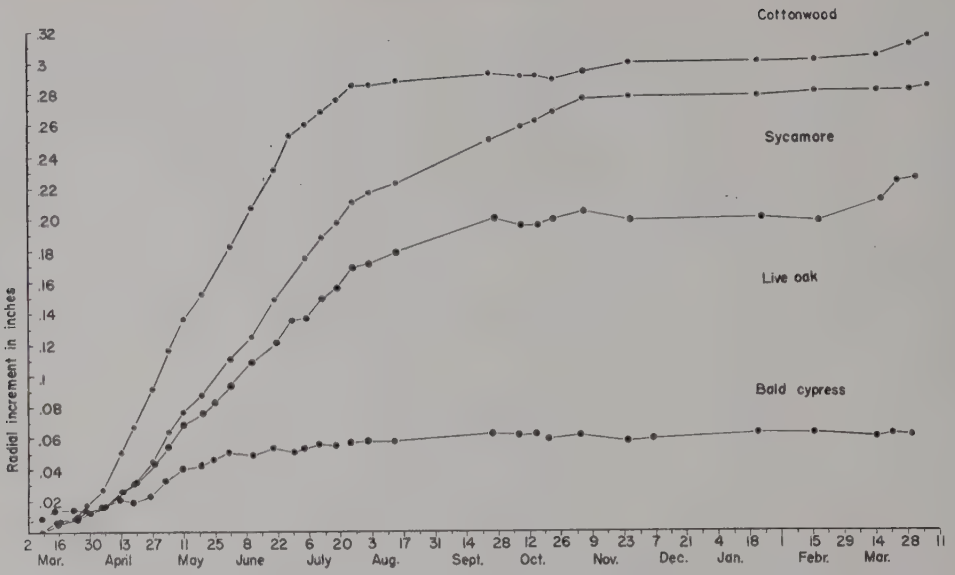

FIG. 1. Mean total radial increase at various times, March, 1951, to March, 1952. Cottonwood, 13 trees; sycamore, 9 trees; live oak, 1 tree; bald cypress, 11 trees.

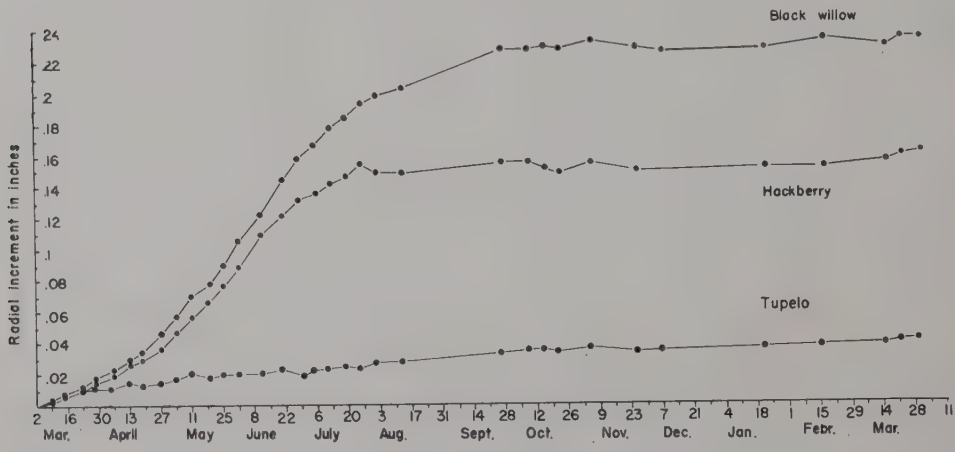

FIG. 2. Mean total radial increase at various times, March 1951, to March, 1952. Black willow, 13 trees; hackberry, 10 trees; tupelo gum, 9 trees.

The week ending July 26, 1951, appeared to be a critical time in the growth of trees in the New Orleans area. In addition to the four bald cypresses mentioned above, other trees which stopped growth at that time included two cottonwoods, one sycamore, three willows, and all ten hackberries. One cottonwod grew to August 2, seven others to September 23, one to October 15, and two to October 23. Five sycamores grew until about September 23, two to about October 7, and the last one grew a little until November 3. Seven willows ceased increase on about September 23, one on October 8, and the other two grew until about October 15. The one live oak increased until September 27.

Just as there was more than a three month lapse between the time when the first and last tupelo gum began radial increase so there was a three month variation between when the first and last ceased to increase. Six trees of this species

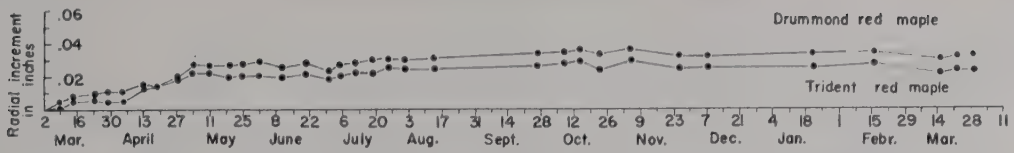
Radial increment in inches
.06
.04
.02
Drummond red maple
Trident red maple
2 16 30 13 27 11 25 8 22 6 20 3 17 31 14 28 12 26 9 23 7 21 4 18 1 15 29 14 28 11
Mar. April May June July Aug. Sept. Oct. Nov. Dec. Jan. Febr. Mar.

FIG. 3. Mean total radial increase at various times, March, 1951, to March, 1952. Drummond red maple, 2 trees; trident red maple, 2 trees.

changed no significant amount after August 4, but three continued to increase to November 4. Growth in the red maples were so slight that it was difficult to determine when they actually stopped. It appears, however, that growth in Drummond's maple had nearly stopped by July 19, but one increased slightly until October 15. One of the trident red maples reached its maximum radius by August 3, but the other increased until October 8.

Length of growing period of the trees

One might suspect that trees would continue to grow as long as temperatures were high enough, which in the New Orleans area would be through November. But the preceding discussion indicates that most trees cease growth long before temperatures are low. Approximate growth periods for each tree species are as follows: cottonwood—four to seven months, a majority grew about six; sycamore—four to seven months; willow—five to eight months, a majority about seven; live oak—one tree grew about seven months; hackberry—all grew about four four months; bald cypress—two and a half to four months; tupelo gum—five months; Drummond red maple—five to seven months; trident red maple—five to seven months. The longest-growing tree was a willow in the cypress-tupelo swamp which grew for eight months, the trees with the shortest growing season were bald cypress.

Period of maximum growth

Reference to Figures 1 to 3 will show that a majority of the species increased in radius at a rather uniform rate during a significant part of the growing season. The time of most rapid, rather uniform growth is here called the period of maximum growth. On the curves it is represented by a steep, nearly straight slope. Before and after this period growth is less rapid. Cottonwood, sycamore, willow, hackberry, and to some extent bald cypress, follow this pattern of growth. Tupelo gum and the red maples grew too slowly and too little to permit recognition of a period of maximum growth. The period of maximum growth, with the part of the total for the season which occurred during this period, is given in column 4 of Table I.

Live oak has the longest period of maximum growth, 109 days, during which time it grew 70 per cent of its total for the year. Sycamore had a maximum growing period of 100 days, with 65 per cent of the season's total formed then; black willow, 91 days and 63 per cent; cottonwood, 77 days and 73 per cent; hackberry, 69 days and 64 per cent. Bald cypress had the shortest period of maximum growth, 33 days, during which time it increased 45 per cent of the total.

The present use of the term maximum growth is different from that by Jackson (1952), who arbitrarily includes all growth between 5 and 90 per cent of the total for the year as occurring during a period of maximum growth.

Time of half-growth

What may be called the time of half-growth, when fifty per cent of the season's growth is attained, is recorded for each species in column 5 of Table I. The slowest growing species, the maples, attained half-growth before the end of April, bald cypress by May 1, and tupelo gum by May 5. Cottonwood, which heads the list in total growth for the season, was fifth in reaching half-growth, May 22. The other three species reached half-growth in June, sycamore last of all.

The number of growing days to reach half-growth, that is days between growth onset and half-growth, is also recorded for each species in column 5 of Table I. There seems to be a limited correlation between the number of growing days to reach half-growth and the number of calendar days elapsed in the year before half-growth; there also seems to be limited correlation between these time summations and the total growth for the season. The last four species listed in Table I required a small number of days to reach half-growth, it was attained early in the year, and they grew a small amount during the total year. The first five species in the table grew more days to attain half-growth, it was attained later in the year, and they grew more during the total season.

Leaf development in relation to radial increase

Each time that measurements of radii were made observations were also made on the condition of the leaves. In column 6 of Table I is given the approximate time during which leaves

TABLE I. *Results of measurements of radial growth in nine species of forest trees, with correlative data on leaf development*

Species	Mean total radial increase in inches, 1 year	Date radial increase began	Date radial increase ceased	Period maximum increase, and per cent total during the period	Date when half-growth reached; calendar days to date	Time leaf development, from bud to maturity	Development leaves at start of radial increase	Development leaves when maximum growth began
Populus deltoides, 13 trees	0.315	March 14-24	July 26-Oct. 23	April 5-June 22 (77 days); 73%	May 22; 59-69 days	March 1-April 30	1/3-1/2	3/5-4/5
Platanus occidentalis, 9 trees	0.282	March 24-April 6	July 26-Nov. 3	April 15-July 25 (100 days); 65%	June 18; 73-86 days	March 1-May 10	1/4-3/4	Mature, to a week past maturity
Salix nigra, 13 trees	0.234	March 14, swamp; April 27, batture	July 26-Oct. 15	April 13-July 13 (91 days); 63%	June 7; 65-85 days	Febr. 1-April 1, swamp; March 15-May 4, batture	3/4 to full	4/5 mature, to a week past maturity
Quercus virginiana, 1 tree	0.225	Febr. 25	Sept. 27	April 6-July 25 (109 days); 70%	June 7; 102 days	Febr. 1-March 30	1/2	A week past maturity
Celtis laevigata, 10 trees	0.155	March 14-21	July 26	April 20-June 29 (69 days); 64%	May 25; 65-72 days	March 1-May 5	1/3-1/2	3/4
Taxodium distichum, 11 trees	0.061	March 9-April 20	June 1-July 26	April 27-May 30 (33 days); 45%	May 1; 10-53 days	Febr. 20-April 15	1/2-3/4	Fully mature (One tree at 1/2)
Nyssa aquatica, 9 trees	0.039	March 15-June 30	August 4-Nov. 4	Indefinite	May 5;	March 10-May 10	1/3-full	Mature, to a month past
Acer drummondii, 2 trees	0.032	March 10	July 19-Oct. 15	Indefinite	April 25; 40 days	Febr. 20-April 1	4/5	Mature, to several days past
Acer rubrum var. *tridens*, 2 trees	0.024	March 10	August 3-Oct. 8	Indefinite	April 13; 34 days	March 1-May 5	4/5	Mature, to several days past

were developing. Most species required about two months for the complete process of leaf opening and expansion. Live oak, and willows in the cypress-tupelo swamp, began to put out leaves, leaves emerged from buds, about February 1; bald cypress and Drummond maple began about February 20; other species began from March 1 to March 10.

That auxins, produced in developing buds and leaves, influence the initiation of cambial activity is generally accepted. Fraser (1952), reporting on increase in diameter of trees in Ontario, cites literature on the subject of auxin production in leaves and buds and also describes his own work which lends support to the theory.

In this study, it was found that, for most trees, radial increase began before leaves were fully expanded. (Column 7 of Table I.) The degree of leaf maturity at onset of radial increase varied from about 25 per cent, for certain sycamores, to full maturity in some willows and tupelo gums. The average for all trees was about 50 per cent.

The period of maximum growth did not begin in most cases until leaves were fully mature. Cottonwood and hackberry began to grow at the maximum rate when leaves were about 75 per cent developed; sycamore and willow varied between maturity and a week past maturity; the one oak began maximum growth a week after leaves were fully expanded. Most cypress trees began maximum growth at about the time leaves reached maturity, but one tree began when they were half mature. The information is summarized in column 8, Table I.

A comparison of these observations on the relation between growth onset and leaf development, with those of Jackson (1952) shows there is a difference in the behavior of trees in different areas. Jackson found that near Athens, Georgia, radial growth of hardwoods and bald cypress did not start until 20 to 30 days after leaves were full grown. By contrast, in this study it was found that radial increase began when leaves were about half-grown. The explanation for this difference is not entirely obvious, but it is possible that it is related to the slow rate at which leaves develop in the New Orleans area or, that trees in the two areas are genetically distinct in certain respects.

According to Meyer and Anderson (1952) "— resumption of cambial activity is activated by auxins which move in a basipetal direction in stems from developing buds." Where leaf development is rapid the effect of auxins may not be evident in the cambium until after leaves have reached maturity. Where leaf development is slow, about two months required for the trees in this report, it would be possible for auxins produced in early stages of bud development to move down to the bases of the trees and stimulate cambial activity before leaves had completed development. It also may be that the ecotypes of some of the species in the New Orleans area are distinct from those in the Athens, Georgia area, in regard to the size of leaves at the time that cambial activity begins. This in an involved relationship and many more observations must be made before any definite conclusion can be reached.

Growth and External Factors

A review of the literature indicates that under controlled conditions many external factors may limit growth. However, workers who have made detailed measurements of growth of trees in the forest have generally limited their observations on environmental factors to a few, usually only temperature and water.

Byram and Doolittle (1950) believed that by June soil moisture began to be a limiting factor in the growth of a tree of *Pinus echinata* near Asheville, North Carolina. The pine did continue to grow until August 25. Friesner and Walden (1946) measured the growth of two trees of *Pinus strobus* in Camden, Maine, and concluded that temperature controlled the initiation of radial growth and was probably the limiting factor in determining cessation of growth. Bonck and Penfound (1944) reported on elongation of twigs of trees growing on the batture of the Mississippi River near New Orleans (about eight miles from the site of these studies) and concluded that water shortage was no problem. Daubenmire (1949), in a study of seventeen species of angiosperm and gymnosperm trees growing near Moscow, Idaho, found that, in several species, initiation of growth bore no close relationship to maximal or minimal temperatures. In many instances, growth began at a well-defined period, suggestive of photoperiodism. There is no strong evidence that photoperiod controls growth acitvity of any of the trees in the New Orleans area but, as will be pointed out, the behavior of some trees suggests that photoperiod may play a part.

There was nothing unexpected in the time at which most of the trees of this study began radial increase, the first in late February, many in March. It is believed these began radial growth as soon as temperatures were high enough. Definite influence of temperature on willows is seen in the fact that those growing on the batture began growth about five weeks after those in the swamp. That some trees, notably tupelo gum, did not begin growth until later, even into June, was unexpected. It may well be that some other factor, such as photoperiod, is influential with these.

Quite unexpected was the early cessation of radial growth by some of the trees. Some bald cypresses grew not at all after June 1, and many trees of this and other species ceased growth in July. The suddenness with which all hackberries ceased growth in July was quite striking also. It is believed there was no shortage of water during this early summer period, certainly not in the cypress-tupelo swamp. Two factors suggest themselves as possible influences in determining the early cessation of growth of some species, prolonged high temperatures and photoperiodic influences.

In the New Orleans area, high summer temperatures usually persist from about May 20, through September, with little variation. Extremely high temperatures are not reached but high ones are maintained. The following monthly, maximum-minimum, Fahrenheit temperatures, for the summer of 1951 indicate this: May, 91-59; June, 92-70; July, 96-73; August, 96-72; September, 96-66; (U. S. Weather Bureau Station at Moisant Airport, about 5 miles from sites of this study). Prolonged high temperatures might cause the trees to respire at high levels, thus using food excessively fast, or they may result in the breakdown of enzyme systems, including auxins, which are essential for continued growth.

Bald cypress, and all the other species, began growth during a time of increasing day length. But five bald cypress ceased growth by June 1,

while days were still growing longer. It may not be impossible but it does not seem likely that increasing day length would first help initiate growth and then, when days are longer, inhibit it. The case of hackberry, in which all individuals ceased growth at almost exactly the same time, suggests the influence of some common factor. Certainly photoperiod could be such a factor. Temperature could also. Members of the other species ceased growth at irregular times and there is no strong evidence for or against the possible importance of photoperiod.

Summary

Measurements of radial increase of 70 trees, in nine species, growing in southern Louisiana, were made at frequent intervals over a period of a year. Of the nine species, cottonwood grew the most, with a radial increase of 0.315 inch, and trident red maple the least, 0.024 inch. Live oak began growth earliest, in February. A majority of all trees began growth in March and April, but a few individuals did not start until June. Bald cypress was the first to cease growth, some individuals by June 1; one sycamore and several tupelo gums grew until early November. Usually, individuals of a species ceased growth at different times, but ten hackberries stopped at the same time. The length of the growing period, the period of maximum growth, and the time of half-growth are given for each species. Leaf development is correlated with initiation of cambial activity. Most trees began growth before leaves were fully mature. It is believed low temperatures limit initiation of growth of trees which start in February and March. Most trees cease growth in summer while temperatures are still high. There appears to be no shortage of water and it is suggested that continuous, high, summer temperatures or, possibly, photoperiodic influence may play a part in causing cessation of growth.

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NOTES AND COMMENT

A LIGHTWEIGHT PISTON SAMPLER FOR LAKE DEPOSITS[1]

Introduction

During the past few decades, much attention has been given to the design of lake and sea bottom coring apparatus. Samplers for specific purposes have been brought to a rather high degree of refinement (Jenkin and Mortimer 1938, Kullenberg 1947, Wilson 1941), but the better types are all heavy, while the lighter hand-operated models, the Davis and Hiller samplers, are slow to operate and do not take an undisturbed sample.

During pollen analytic studies on the Arctic coastal plain of Alaska, need arose for a sampler which would combine the lightness of the standard equipment with some of the efficiency of the special samplers. A piston corer, inspired by the Kullenberg deep-sea device, but operated by manual thrust in a casing instead of by free-fall from a winch, was constructed and used successfully in the field.

Construction and Use

The apparatus consists of a thin-walled tube of high-strength aluminum alloy, attached to extension rod of the excellent type described by Lichtwardt (1952). Inside the tube is a close-fitting piston to which a flexible steel cable is attached at the upper end.

The construction details of the coring apparatus are shown in the accompanying plate. The rod used was of slightly greater diameter than Lichwardt's original, and had sleeves of aluminum alloy instead of iron. The sample tubes are long enough to accommodate the piston and a one-meter core. They are held on to the extension rod by a special fitting and a tapered pin.

Because the extension rod is so flexible in lengths of more than a few metres, it is very desirable to use the apparatus inside a casing. A brass and aluminum casing in one-meter lengths, with bayonet-clutch joints, was used in the Arctic. It was dependable, but heavy and expensive to construct. Vallentyne (1955) has found that ordinary stovepipe will serve the purpose.

The casing is lowered from the center of the raft until the lower end is anchored in the mud. The upper end is then lashed to the raft. It is not necessary to case the walls of the sampling hole itself, but only to provide a casing in the water, so that the extension rod will not bend when thrust is placed upon it.

Before beginning a sampling drive, the piston is brought to the lower end of the tube where it is lightly held in place by two spring-pins. The sampler is then lowered to the level at which sampling is to commence, usually the surface of the lake bottom. During this operation the piston cable is payed out freely, but once the sampling level is reached the cable is clamped in a vise so that the piston cannot move any farther down. Then the tube is pushed down around the piston by pushing on the extension rod. As it goes down the tube fills with lake sediment; the piston prevents compression of the sample during the drive and prevents the sample from falling out while the sampler is being lifted up again.

The apparatus is hoisted up to the surface, the tube is removed and replaced by an empty one, the vise is loosened, one meter of cable is fed through the jaws, it is clamped and the operation is repeated. Up to fifteen consecutive meters of lake sediment have been sampled in this way.

For work on lakes, a portable raft is used which consists of a marine plywood platform placed across two war-surplus inflatable six-man rubber dinghies. The platform has a hole in the center through which the apparatus is lowered, and several cleats on its surface to which the necessary mooring lines are attached. A third dinghy is used as a tender and a three-horsepower outboard motor is used whenever possible for maneuvering the raft into the drilling position.

If the piston rings are worn, so that the piston does not fit closely against the wall of the sample tube, a certain amount of water will leak in around the piston and a corresponding volume of sediment will be lost. It is well to carry an abundant supply of spare piston rings and to replace them as necessary. Any water that does leak in must be carefully poured off before the tube is stoppered at both ends for shipment to the laboratory. Cork stoppers have proved somewhat more convenient than rubber ones for sealing the tubes.

The whole apparatus, including raft and outboard, but not anchors, which can usually be improvised on the spot, weighs only about one hundred and fifty kilograms. The constituent pieces are small enough for convenient back-packing. It is most efficiently operated by two men, but one man can use it in favorable weather. Assembly and disassembly take about three hours and about fifteen minutes are required for each one-meter sample, although these times vary with the weather conditions and the depth of water in which the work is being done. At temperatures above freezing, with wind speeds of less than twenty miles an hour, an experienced pair can take a complete core through an average post-glacial deposit in one day.

This sampler has been used with success in gyttja, clay, silt, and fine sand. It will penetrate coarse gravelly sand with difficulty. So far it has not been tried on fibrous peat. In the sediments which it penetrates easily, it take a virtually complete undisturbed core. This is a great help in any work which demands close-interval sampling and also permits the counting and measuring of graded beds and color bands in sediments where they would be missed with Hiller or Davis samplers. The

[1] Funds for the construction of the sampler were provided by Contract SAR/NONR-340(00) between Yale University and the Office of Naval Research of the United States Navy. The instrument itself was constructed in the Stirling Chemical Laboratory machine shop of Yale University under the supervision of Mr. Karl Haglund. The author is indebted to Mr. Haglund and also to Dr. E. S. Deevey, Jr., of the Osborn Zoological Laboratory of Yale University, for many helpful suggestions which are embodied in the design. A description of the apparatus was submitted to the Department of Zoology, Yale University, as part of a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Field testing was carried out at the Arctic Research Laboratory, Point Barrow, Alaska. The manuscript was prepared during tenure of a National Research Council of Canada Postdoctorate Overseas Fellowship at Cambridge University.

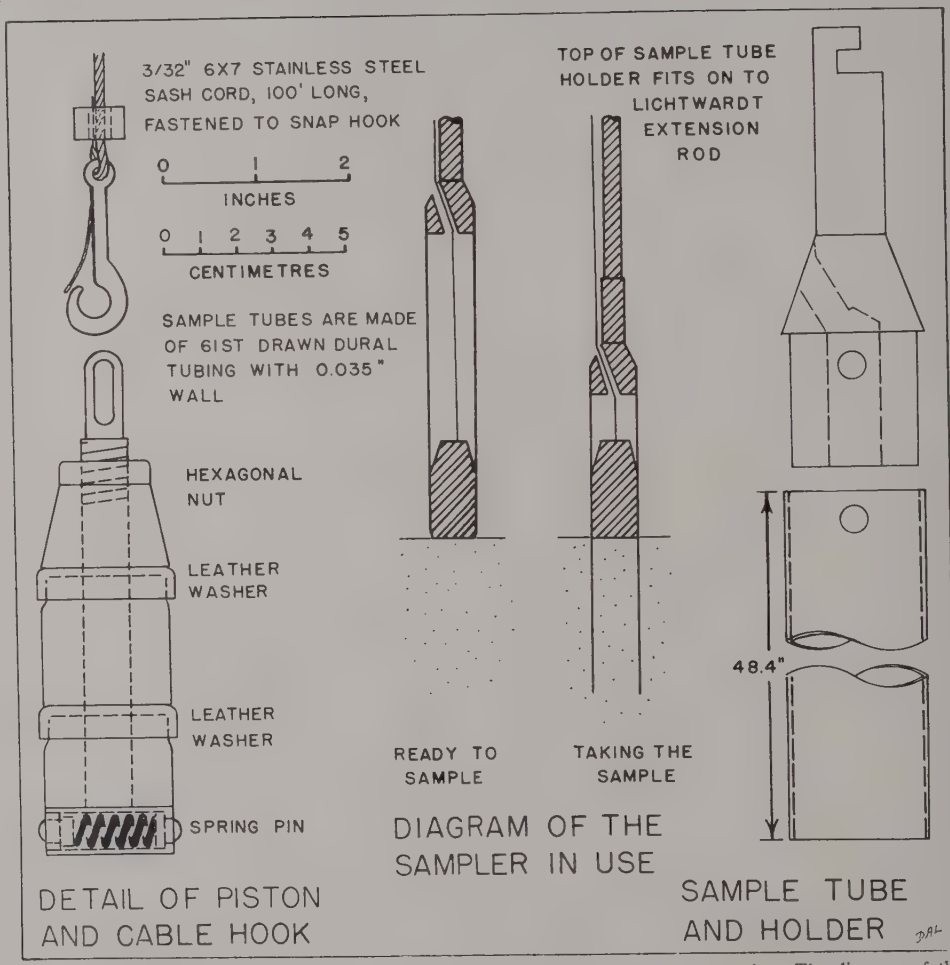

FIG. 1. Diagram and construction details of the piston sampler for lake deposits. The diagram of the sampler in use is not to scale.

undisturbed, uncontaminated, nature of the sample should be a great help in bacteriological and chemical studies of lake sediments as well.

Several possible improvements have not yet been tried out. A sampler of larger diameter would be of value in chemical work and in sampling for C^{14} analysis. The resistance which must be overcome in forcing a sampler of this type into the mud depends chiefly upon the surface area of the sampling tube wall. This increases arithmetically with increase in the diameter of the tube, and it is quite possible that a sampler of a decimeter or more in diameter could be pushed into lake sediments by hand. Larger diameter would also permit a sampling tube longer than one meter to be used, which would be an advantage under some circumstances.

Since this note was first prepared a number of important modifications in the design of the apparatus have been introduced by Dr. J. R. Vallentyne. His sampler is cheaper to construct and does not depend upon spring pins. It will penetrate very stiff sediments more easily and reliably than this one, and could be used with a jar-stem, which this one could not. The Vallentyne sampler and its use are fully described elsewhere in this journal.

SUMMARY

A new lake bottom sampling device has been constructed which takes an undisturbed and uncontaminated sample of lake bottom sediments. It is light in weight and can be operated by a single man. For lake sediment study, particularly in remote areas, these characteristics make it preferable to any of the standard core samplers.

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A MODIFICATION OF THE LIVINGSTONE PISTON SAMPLER FOR LAKE DEPOSITS

Introduction

The effectiveness of the Livingstone piston sampler (Livingstone 1955) in obtaining an undisturbed core of sediment was demonstrated to the author when he assisted Livingstone in taking a core from Lower Linsley Pond, Connecticut. Two noteworthy observations were made at the time of sampling:

1. The lower part of the core contained a series of alternating brown and black bands.
2. Samples extruded into the lake water remained floating for several hours.

The first observation showed that the sampler could preserve sediment laminations. It was concluded from the second observation that the sampler was sensitive enough to retain gases lodged in the sediment, for otherwise the samples should have had a density greater than unity.

The Livingstone sampler so impressed the author that he decided to have another made for his own use. From the start, however, it was apparent that the cost of the original was prohibitive. Some time was therefore spent in designing a simpler type of piston sampler. Through the efforts and interest of Mr. R. D. Bradfield, instrument maker at Queen's University, the author's first design was modified until a strong and effective piston sampler resulted. It is a pleasure to acknowledge the help and advice of Mr. Bradfield as well as his work on the construction of the sampler. This work was supported by a grant from the National Research Council of Canada.

Description of the Sampler

The new sampler combines features of the Livingtone sampler with those of the Davis borer. Figure 1 shows the design of the sampler. *The piston rod* (Fig. 1, A and B) is made of brass rod about 5 feet long. It is fitted at the lower end with a spring catch similar to that of the Davis borer. A sliding collar with screw can be tightened at any level on the piston rod. *The head piece* (Fig. 1, C) is attached to the sample tube by three screws. The head piece also has three holes, one for the piston rod, one for the piston line and one for the lowering line. *The piston pieces* (Fig. 1, D, F, G and H) are four in number plus a leather washer (Fig. 1, E). The upper piece (D) has a bevelled cup (D-1) which receives the lower end of the piston rod, and also has an L-shaped hole (D-2) for the piston line. This hole is widened at the end (D-3) for a knot tied in the piston line. The other parts of the piston pieces are self explanatory. The sample tube (Fig. 1, J) is shown with the other parts attached to it.

In the construction of the sampler, care should be taken to have a loose fit between the head piece and the piston rod. If the fit is too tight, sand grains may prevent free movement of the piston rod when taking a sample. For the same reason there should be a play of about one mm. between the catch on the piston rod and the top of the head piece. In the first sampler constructed, there were two leather washers, but it was later found that one was sufficient. The top of the piston rod is threaded to receive the steel connecting rods commonly used with the U.S.G.S. modification of the Davis borer. It should be possible to use Lichtwardt rods with the sampler by making an adapter that would screw into the top of the piston rod.

In our work we have found it convenient to remove samples from the tube at the time of collection. If other workers prefer to retain samples in the tubes in which they were collected, then the hole for the lowering line (Fig. 1, C-3) should pass vertically through the head piece. The head piece could then easily be removed from the sample tube after taking each sample. In the present sampler the lowering line passes through both the head piece and the sample tube.

The complete sampler as given above was made at a cost of $50.00. This cost included labor and all materials except the sample tube.

Operation of the Sampler

The sampler is operated in two different ways depending on whether a loose surface sediment or a compact sub-surface sediment is being sampled. In either case, the sampler is first assembled. A wire piston line extends from the piston to about five inches beyond the top of the sample tube. A loop is knotted on the upper end of the piston line and any length of wire may be attached to this by means of a catch. The piston rod is lowered into the bevelled cup of the uppermost piston piece. The bevelled nose piece of the piston protrudes from the sample tube and the brass collar on the piston rod is tightened in position. The sampler is then ready for operation and need not be taken apart again.

The procedure for sampling a loose, near-surface sediment is first to lock the bottom of the piston rod to the head piece, leaving the piston at the bottom of the sample tube. The sampler is lowered through the water by holding on to the extension rods or the lowering line. When the desired depth is reached, the piston line is clamped to the boat or raft and the rods pushed down until the sample has been taken. The sampler is raised and the sample extruded into a half cylinder made from sheet aluminum. When the depth of water is first known, it is possible to collect a sample which has water in the upper part of the tube and sediment in the lower part. The seal of the piston together with the friction of the sediment sample against the tube wall are sufficient to retain the sample, providing that the column of water is less than 30 cm. long. The above procedure is used for loose sub-surface sediments when there is no danger of the piston rising in the sample tube before the desired level is reached.

The procedure for sampling more solid sub-surface sediments is to let the bottom of the piston rod rest in

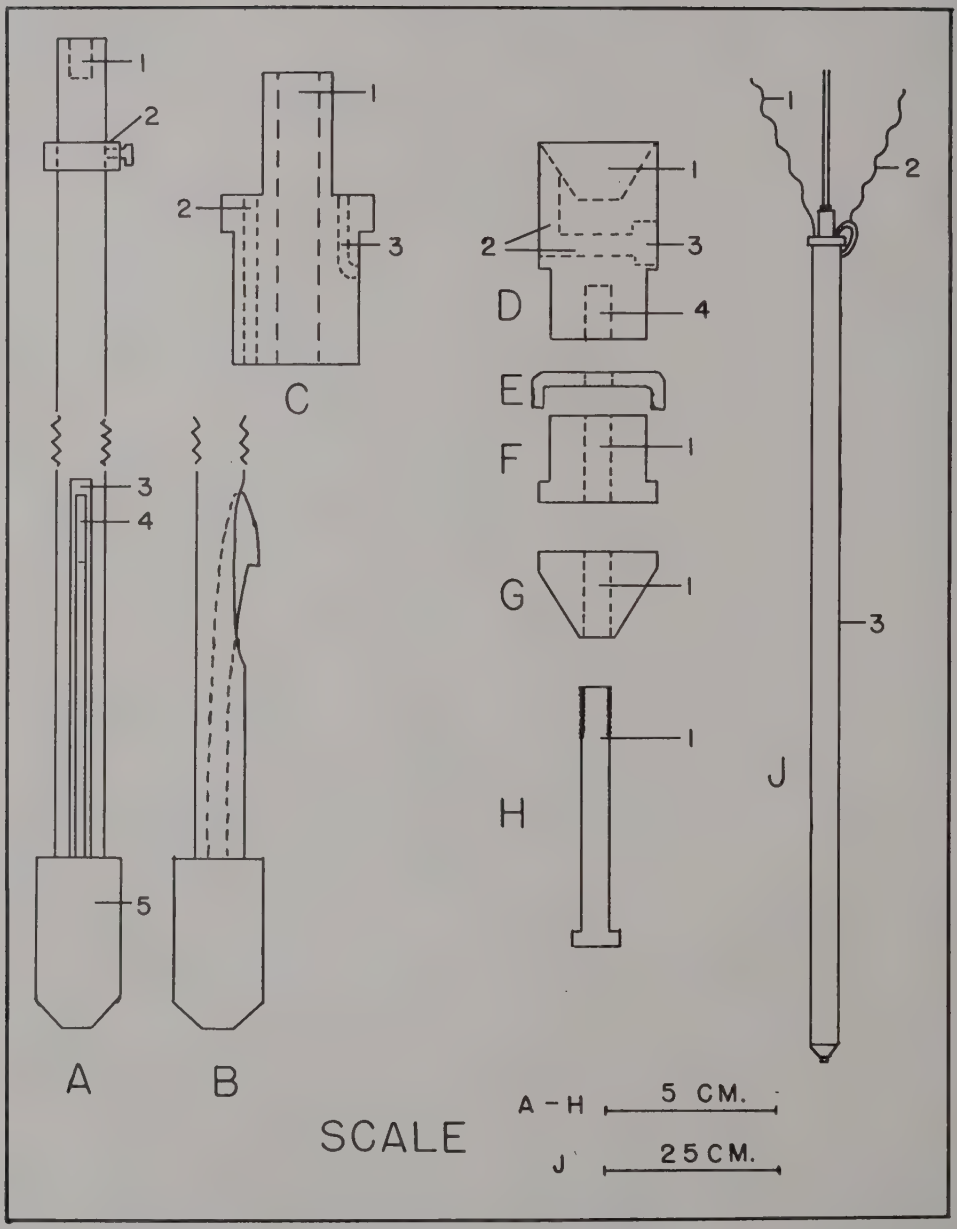

FIG. 1. A modification of the Livingstone piston sampler for lake deposits. A, piston rod with threaded hole (1), brass collar with screw (2), slit (3) for catch (4), and bottom piece (5) of wider diameter; B, bottom part of piston rod turned 90° from that shown in A; C, head piece with a hole (1) for the piston rod, a hole (2) for the piston line, and a hole (3) for the lowering line; D, uppermost piston piece with bevelled cup (1), L-shaped hole (2) for piston line, this hole widened in diameter at the end (3) for a knot tied in the end of the piston line, and a threaded hole (4) for the piston bolt; E, leather washer; F, middle piston piece with hole (1) for piston bolt; G, bevelled nose piece of the piston with hole (1) for piston bolt; H, piston bolt with a threaded upper end (1); J, the assembled sampler with piston line (1), lowering line (2) and sample tube (3).

the bevelled cup of the uppermost piston piece, and then to lower the sampler by the lowering line. With hard sediments, it is necessary to push on the connecting rods until the desired level has been reached. Since this force is directed against the piston there is no danger of the piston rising prematurely in the sample tube. When the desired level has been reached, the piston line is secured to the raft. The extension rods are pulled up slowly until the catch is heard to lock to the head piece. The friction of the sample tube against the surrounding sediment is sufficient to keep the sample tube in place while the rods are being raised. The sample is collected by pushing down on the extension rods as given above for a loose sediment.

The sample tube is cleaned by pulling out the combined piston pieces and rinsing the tube in lake water. The sampler has been found to operate well in gyttja, clay, silt and, with difficulty sand. Though it is difficult to push the sampler through compact clay, it is often harder to pull it back up, presumably because of a suction which develops below the sampler. We have found it necessary to have a tripod car jack bolted to the raft for use in pulling the sampler out of clay. The suction is broken when the sampler has been raised six inches.

The sampler takes in undisturbed sample one meter in length. Adjacent samples taken from sub-surface varved clay show that the varves can be matched to within a few mm. In the sediments of Lake Opinicon, Ontario, we have taken three separate samples of a sedimentation discontinuity where the sediment abruptly changes from a silt-clay to a gyttja (65% ignitable matter) in a vertical distance of one mm.

In taking cores from deep water, it is of course necessary to use a casing to enclose the borer and extension rods. At the suggestion of D. A. Livingstone we used connected pieces of stove pipe as the casing, and found them well-suited for the purpose. Bent nails serve to connect the stove pipe at joints.

If a release pin is attached to the piston line (see Emery and Broussard 1954), then the lowering line becomes unnecessary. We have also found that the low cost of our sampler is partly due to the low labor charge of the instrument maker.

Comparison with the Livingstone Piston Sampler

It may be helpful to the reader to list the advantages and disadvantages of this piston sampler as compared to Livingstone's.

Advantages:

1. The cost of the author's sampler is less than that of the Livingstone sampler.
2. With proper use there is no distortion of the upper 5-10 centimeters of the sample as is the case with the Livingstone sampler.
3. All the force of pushing on the extension rods is taken by the piston and head piece of the sampler. There is no danger of the piston rising prematurely in the sample tube as there is with the Livingstone sampler.
4. The design of the author's sampler permits the use of a falling weight to force the sampler through a compact sediment.

Disadvantages:

1. In taking sub-surface samples with the author's sampler it is necessary to use a lowering line in addition to the piston line. The presence of two wires in the casing is noxious since they may entangle.

Summary

A modification of the Livingstone piston sampler is described. The sampler employs the piston feature of the Livingstone device in conjunction with the rod and locking mechanism of the Davis borer. The sampler is used in different ways for loose and compact sediments. Advantages over the Livingtone sampler are: (1) reduced cost, (2) no distortion of the uppermost part of the sample, (3) no danger of the piston rising prematurely in the sample tube, and (4) the design permits the use of a falling weight to force the sampler into a hard sediment. The main disadvantage is that two wire lines are necessary instead of the single line of the Livingstone sampler.

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OUTLINE FOR AN ECOLOGICAL LIFE HISTORY STUDY OF A FISH[1]

Introduction

This paper, another in the series of life history outlines prepared under the sponsorship of the Committee on Life History Studies of the Ecological Society of America, is a modification of an outline that was made to guide my own research. Gill's (1910) brief schedule for observation provided the original basis to which additions and revisions have been made over the years. The latest reorganization brought about a closer correlation between the portion on the fish with that on the environment in line with the desires of the Committee on Life History Studies. While the outline itself is, with suitable modifications and additions, usable for a study of the life history of most fish, the remainder of the paper is more directly applicable to the study of North American fresh water fishes. This paper is especially intended to aid beginning graduate students.

[1] Funds other than those budgeted for Ecology have been used to defray cost of excess pages in this article.

Literature

The relevant literature is large and is growing rapidly. Unfortunately, much, if not most, of the published information is scattered through a variety of papers that are only indirectly related to life history studies. One will find it worth while to examine, in addition to those papers that by their titles obviously relate to the life history of the species in question, the following: papers that treat of the life history of the several ecological associates of the species; revisions or monographs of the appropriate genus, or higher group; state or other local lists that include fishes from throughout the known range of the species and from adjacent areas; synecological re-

ports, especially those dealing primarily with aquatic communities; and papers in economic biology such as pollution and water analysis studies, efforts to control insects through the use of fishes as predators, hatchery procedures and results, analyses of stocking, and various other phases of fisheries and wildlife management. Appropriate reference to the literature of geology, physiography, parasitology, bacteriology, psychology, physiology, and, of course, of limnology and oceanography should be made. The literatures of entomology, herpetology, ornithology, mammalogy, and other fields often contain scattered remarks pertinent to a given life history study.

In addition to the usual bibliographic sources that are available to zoologists in general, there is available to ichthyologists Dean's (1916-1923) monumental Bibliography of Fishes, a cumulation of literature of ichthyology to the year 1914. This work was continued in card form to 1938 by Dr. E. W. Gudger of the American Museum of Natural History in New York. The cards are available for use at the museum. Unfortunately, there appears to be no prospect of their publication. Carlander's (1954) compilation of the vital statistics of the fresh-water fishes of the United States contains a large bibliography pertinent to the life histories of the fishes of that region.

Other information is available, but is difficult to locate because it is not compiled by the usual bibliographic journals. These include theses and dissertations, mimeographed reports to state or other governmental agencies, and articles, which though intended for the layman, are often written by well-informed specialists. A list of dissertations that relate to fisheries from North American schools has been prepared by Carbine (1952).

In searching the literature one should be prepared to recognize references to a given species under a variety of generic, specific, and trivial names, and, occasionally, to recognize the application of the same name to different species by different authors. This is true not only for the common name but also for the technical name. As a result of misidentifications, and of the alternate activity of splitters and lumpers, ichthyology has at least its share of nomenclatorial confusion.

Unit of Study

Since most species of fish exist as more or less isolated populations, conceivably one might approach a life history problem from one of three ways: by an intensive study of a local population; by a more diffuse study that would include several to many such populations, none of which would be treated intensively; or by a concentrated study of one or a few individuals from fertilization till death. This last approach, which is largely impractical with the fishes, will not be considered further. The prime advantage of the diffuse approach is that the results are likely to be more "typical" of the species as a whole, while that of the intensive approach is a reduction in the complexity of the problem. For example, such small but definite seasonal changes in the preferred microhabitat, as a shift from one pool type to another, are much more readily detected during an intensive approach because one is able to become better acquainted with the finer details of the habitat and its biota. Complications, introduced by variations in the genetic composition of the populations such as are indicated by modern evolutionary studies, are avoided. Also in favor of the use of the local population, rather than the species as a whole, as the basic unit of study, is the fundamental importance of the local population in evolutionary and synecological studies and thought. While each approach has merit, a combination of the two is undoubledly superior to either alone; an intensive study of a local population, supplemented by an examination of other populations, provides a good insight into the finer workings as well as some concept of the variation that exists in growth, behavior, etc.

The species should be followed throughout its ramifications in the community and through each of the communities in which it occurs. In order to determine the extent of, the significance of, and the modes of avoiding competition, predation, etc., some study of the other major forms in each community is essential. This is not to suggest that a synecological approach be used, but that a certain amount of comparative data on the influential forms in the community is useful in understanding the niceties of the ecological relationships.

The advantage of obtaining perspective by studying two or more species in the same group should not be overlooked. For example, transient or ill-defined behavior patterns are sometimes more readily recognized if some knowledge of related forms is available. Or, minor differences in behavior or in habitat selection are most obvious when two similar species are compared, especially if they occur in the same body of water as sometimes happens both naturally and through the agency of man.

Equipment and Methods

The many techniques and types of equipment that are suitable for ichthyological research are too numerous and too diverse to be treated at length here. For the most part, the literature citations are intended to serve as examples that will suggest further readings on the subject. The references in these papers will ordinarily lead to the more important earlier works. Fortunately for the beginner in the field, there are several compilations of techniques useful in life history research. Two of a general nature that provide introductions to the literature of ichthyology as well as to some basic techniques are those of Lagler (1952) and Rounsefell and Everhart (1953). Other compilations of a more restricted scope will be mentioned in appropriate sections.

Work in both field and laboratory is essential to a life history investigation of a fish. In the ideal situation the laboratory would be located in the immediate area of field work so that outdoor and indoor studies might be thoroughly co-ordinated throughout the seasons. Besides facilitating many efforts, this arrangement would help to minimize the all too common tendency to concentrate field work into the warmer periods of the year. The necessity for the study of field conditions in winter has been emphasized by Hubbs and Trautman (1935).

The equipment that is required in field work will vary tremendously with the habitat, with the particular phase of the life-cycle under study, and with different species. The equipment that is required indoors is largely either of the type found in most moderately well equipped laboratories or is of the type that can easily be manufactured.

Methodology as a whole has not been standardized, nor is it particularly desirable that it be so. The methods chosen by the individual worker should be adapted to the species in question. The early, purely observational studies should be supplemented wherever possible by experimentation. Proper controls and quantitative methods are essential to both types of approach. For suggestions as to the respective roles of observation and experimentation and for suggestions as to the proper attitudes and

precautions that should be taken, the reader is referred to Reighard's (1910) classical account of the methods for studying the habits of fishes and to Schneirla (1950). Further suggestions as to procedures of value in the study of animal habits may be found in the reviews by Collias (1950), Lorenz (1950), Riess (1950), and Tinbergen (1951, 1953). Definitions of some terms used in behavior studies may be found in Thorpe (1951).

Thought should be given in advance to the making and storage of records in order that they will be convenient to use and adequate for the purpose. The beginning student will find it well worth while to heed the suggestions regarding the making of records by Reighard (1910) and Schneirla (1950). Check or form sheets are valuable both as time savers and as mnemonic devices for routine work in the field and laboratory. Since large numbers of individuals are often treated in ichthyological life history work, punched cards or comparable techniques should be considered. For moderate numbers of specimens, the author finds plain five by eight inch cards or sheets of paper to be satisfactory for sorting and compilation.

A technique that has had wide application to many phases of life history work is the marking or tagging of live fish to facilitate later recognition. Marked fish have primarily been used to determine: the extent of movement, migration and homing; the densities of populations; rates of growth; rates of mortality or survival; and the effectiveness and other results of stocking or transplanting. Methods of marking include the removal of one or more fins, the use of many types of external and internal tags, tattooing, and the use of x-rays. Identification may be to individual or only to group depending on the method used. Rounsefell and Kask (1945) give an excellent, critical account of the techniques and types of tags available. Methods of tattooing are described by Hickling (1945) and the use of roentgen rays by Hasler and Faber (1941).

Habitat

Indications of the significant features of the habitat can be obtained through a correlation of the environmental characteristics with the general and local distribution of the species. Observations that are made during the seasons of stress, or in marginal portions of the habitat, are especially suggestive. Routine habitat descriptions, such as those suggested by Hoover (1937) and Davis (1938) for use in inland waters are of considerable aid. However, one should not place too much reliance on standardized descriptions, but should ever be on the alert for the less obvious, or the less usual, that would be recorded under "remarks." Information in addition to that contained in the general description of the habitat may be necessary if the environment is complex, or if there is a tendency for different stages of the species to occur in different portions of the habitat. Individuals that are tagged or otherwise labelled can be related to appropriate entries in the field notes. Since it is impractical to label many very small individuals, some modification is necessary. A method by which the shifts in habitat of the larval stages may be followed is to make a series of appropriately labelled subcollections, each from a greatly restricted area. This technique is especially useful when several similar forms are present in the area and their identification in the field is either difficult or impossible. The contents of each subcollection can be identified in the laboratory to species and stage and these in turn can be related through the notes to the appropriate microhabitat.

At least in the inland waters, many important characteristics of the habitat can be determined by inspection and with the aid of such simple instruments as thermometers, rules, and stopwatches. Sometimes clues to certain characteristics of the environment can be obtained from those plant or animal associates that are indicative of special conditions such as low oxygen content, high salinity, temperature extremes, etc. More precise determinations require the expenditure of much time along with the use of special methods and equipment. Many of the techniques appropriate for the chemical and physical analysis of the environment are critically described by Ellis, Westfall, and Ellis (1946) and by Welch (1948).

While the preceding methods will aid in the identification of the significant features of the environment, they will yield little more than approximations of the effects of variations in those factors. For characteristics such as bottom type, the aproximations are probably sufficient, but others such as temperature and oxygen should be understood in a more precise way. The reduction to a quantitative basis of the effects of moderate and extreme variations must to a large extent be acquired through the use of the proper experimental and statistical techniques. These should pay proper regard to the relationships with other environmental factors, to time, and to the past history of the experimental fish. Fry (1947) has provided a thoughtful discussion of this phase of the work.

Capture and Preservation of Specimens

The use of both live and dead specimens is essential to a life history study.

The methods suitable for the capture of the eggs and larval stages will depend upon their location, that is, whether they occur at or near the surface, in midwater, or on, or in, the bottom. Hand or tow nets with appropriate mesh supplemented by hand picking from beds in shallow water are most commonly used. The eggs and fry are most easily sorted from the trash while still alive. A white enameled pan, a small perforated spatula, and a syringe pipette are useful in this regard.

The larger fish may (disregarding legal considerations) be captured by such diverse means as seines, trawls, gill nets, weirs and other traps, spears, electric shocking, explosives, poisons, the angle in all its forms, and even the bare hand. Occasionally one can, or must, resort to the use of fish captured by anglers or commercial fishermen.

The identification of the eggs and larvae often presents a special problem because the distinctive characteristics of these early stages are largely undescribed, and the traits that are normally used for the recognition of adults are undeveloped. The problem is further complicated by the occasional presence of two types of young in the same species (Hubbs and Whitlock 1929) and by the presence of two or more similar species in the same area. In fresh waters, at least, it is not uncommon to find two or more species spawning concurrently in the same small area.

Methods available for the identification of the early stages include comparison of field-collected eggs with those obtained from known ripe females and allowed to water-harden, the incubation of eggs of known parentage in order to obtain the later stages, and the collection of extensive series that provide a complete gradation between the unknown stages and those that can be identified with certainty. In addition to size, shape, and the details of external anatomy and pigmentation, the

number of vertebrae is often of value in the identification of larval forms (Fish 1932). Staining techniques to emphasize these structures are described by Hollister (1934). Instead of the usual calipers, ocular micrometers (Applegate, 1950) or calibrated mechanical stages (Doan 1939) are used to measure the eggs and young. A terminology for the larval stages has been suggested by Hubbs (1943).

The larger specimens are best preserved immediately in ten percent commercial formalin and transferred after proper hardening to approximately seventy percent alcohol. Eggs and fry are preserved in more dilute (about two percent) formalin, and may be left in that fluid or else transferred to alcohol. Formalin is not only disagreeable to work with, but it also destroys in time some useful structures such as the growth rings that are found in otoliths and other parts. Sometimes, for reasons of economy, it is not desirable to preserve the entire fish. Scales, stomachs, gonads or other parts may be all that are retained. In this case all the pertinent individual data should of course be observed and recorded before the carcass is discarded.

Observations on Behavior

Observations on behavior may be made in the unaltered habitat, in enclosures that retain the fish within a restricted portion of the appropriate habitat, or in the laboratory. It should be remembered that anything that restricts the free movement of the fish may produce modifications in behavior and that some activities may be in response to chemicals or vibrations not detectable by the observer under ordinary conditions.

When making observations on the behavior of fish, one is faced, in addition to the universal problem of having to be in the right place at the right time, with those problems associated with making observations in water. In shallow waters these include: distortions caused by refraction at the water surface, which are worse when the surface is ruffled; surface glare and reflection; and turbidity, which sometimes makes its appearance as a result of storms many miles upstream. As the water deepens, the problems become more numerous.

By and large, direct observations can be made only in relatively shallow water since bathyspheres and the more elaborate types of diving equipment are available to only a comparative few. Indirect observations at moderate to great depths may be made by means of cameras or even by television (Schultz 1948). Face masks, particularly when supplemented by tanks of compressed air for breathing, are of value in shallow or moderate depths. Many observations can be made in shallow water with little or no equipment. Sometimes one is able by means of sufficiently stealthy movements to approach very close to fish and have them behave in a seemingly normal fashion. This is especially true if one approaches from the direction of the sun. Blinds are occasionally of help. These may be something elaborate or merely a simple shield with openings through which the observer may peer. Another simple, yet effective, device is to erect a few leafy branches behind the observer to simulate a shrub. Field glasses are of value for observing details even when one is relatively close. By suitable modifications, they can often be made to focus at lesser distances than that intended by the manufacturer. The glare from the surface can be reduced by keeping one's back to the sun, by looking into the reflection of some dark object, or by means of modern polarizing materials. The unevenness of the surface can be eliminated by the use of a glass-bottomed box or pail, or by the use of a water periscope. The activities of fish such as sculpins that live under rocks or in cavities may be observed with the aid of a mirror. Additional light may, if needed, be reflected by means of a second mirror. The success of observations made at night with artificial light will depend in part upon the reaction of the fish to the presence of light. Part of my experience in this regard seems to indicate that some species are variable in their response to increased illumination, since they seem to ignore the light during periods of bright moonlight, but not on dark nights.

Since so many activities of fish are strongly influenced by temperature, the problem of following the temperature changes of the water without disturbing the activity is sometimes difficult. A simple and effective solution for use in shallow waters is provided by the use of a dial-type thermometer such as is used in photographic developing. The thermometer may be fastened in place in such a way that the stem is properly immersed while the dial faces the observer who, with the aid of field glasses, can read it without stirring even at a distance of several feet.

Some time and effort spent in the selection of a place for making observations usually pays dividends. Places where the habitat is typical, where the species is reasonably common, where visibility is good, where one can approach without unduly disturbing the fish, and where the observer will be free of disturbance by visitors are generally to be sought. This last is essential because, while fish recover comparatively quickly from the passage of an animal, they often take a half hour or more to react normally after a brash visit by a person. The sight of an individual with field glasses and camera looking into the water rather than into the shrubbery for birds is almost certain to arouse curiosity in his fellow man. Since a few visits can ruin a day's fieldwork, a place should be sought where such disturbances will be at a minimum.

Whenever feasible, the observer should be established well in advance of the expected activity. For example, if there is good reason to expect spawning to occur in a particular area, one should, if possible, be there before any of the fish arrive. This not only avoids disturbing the animals but also allows one to follow the changes in territorial and other behavior that sometimes occur during a daily cycle of spawning.

Food and Feeding Habits

Observations in the field can provide much information concerning the time, place, and manner of feeding, but they can provide little in the way of precise information on the nature of the diet. For the most part this latter is determined by an analysis of the contents of the stomach or, in those forms that lack a true stomach, of the anterior portion of the intestine. At these levels the food organisms are most easily sorted and identified and their bulks are least distorted by differential digestion. Ideally, for ease in sorting and identifying, fish intended for food studies should be captured near the end of a feeding period before digestion has proceeded far. This is relatively easy to accomplish with those species that exhibit well-defined periods of feeding and abstinence, although sometimes the ideal hour is one normally reserved for the investigator's sleep. However, if stomachs are collected only near the end of the feeding periods, other relationships may be obscured. Ordinarily, food analyses require that the fish be sacrificed, but Robertson (1945) has devised a harmless way of extracting the contents from the stomach of a living trout.

Not all methods of capture are equally satisfactory for the purpose of making food analyses since some result in biased samples and others result largely in collections of empty stomachs.

For a proper understanding of the food habits, the identifications of the food organisms should be as specific and as accurate as possible, even though for publication more inclusive categories are used. Identifications are greatly facilitated if a collection of potential food species is prepared. Such collections should contain not only intact specimens, but also examples of those portions that resist digestion longest, such as the head capsules and mandibles of insects and the bones of vertebrates.

The considerable variation in techniques of analysis and in modes of summarization of the data used by different workers reflects not only differences of opinion, but also the difficulties encountered with different types and quantities of food. The relative importance of the various foods eaten by fishes is usually judged by the quantity of each that occurs in the sample. A few workers consider the food that occurs in the greatest number of stomachs to be the most significant (Wickliff 1921). Apparently because different food items may occur with comparable frequency but to obviously different degree, the number per stomach of the several food items may also be given. Tester (1932) found that volumetric studies alone tended to mask the importance of the smaller food items. Leonard and Leonard (1949) suggest that numerical studies may have the advantage if only a small number of stomachs is involved. The importance of considering both volumetric and numerical data has been widely recognized with the result that many reports include both types.

The quantity of each type of food in a stomach is customarily measured by displacement of alcohol or water, but occasionally weight is substituted for volume. The displacement technique is reasonably simple and accurate if the volumes are fairly large and if the number of units to be segregated is small, but is not with either of the reverse conditions. The difficulty of measuring small quantities with reasonable simplicity and accuracy has led some workers to measure only the total contents of the stomach. The percentage of each food item is then determined by inspection and the volumes derived by calculation. Commonly, if the volumes are small, nothing is measured directly. A grid over which the food is distributed to a uniform depth is often employed as an aid in judging proportions by inspection. The values assigned to the several food items are usually those present in the sample. Occasionally, however, an attempt is made to neutralize the effects of digestion by making estimates of the original volumes (Van Oosten and Deason 1938, Raney and Webster 1940). Hess and Rainwater (1939) suggest additional corrections for offsetting the effects of differential digestion.

Food analysis data are usually summarized in such a way as to indicate changes in the diet with changes in the stage of the life cycle, with the size of the fish, and with the season. Two general methods of summarizing volumetric data are commonly employed. Some prefer to consider all stomachs of equal value, while others prefer to weight the individual stomachs according to the amount of food each contains. Weighting is more accurately accomplished if the volumes are actually measured, but is sometimes achieved by rating each stomach according to its degree of fullness. Numerical data are summarized by indicating the proportions of fish found to contain each particular food item and the average number of individuals per fish.

Many of the problems that relate to food are still in the exploratory stage. These include such basic investigations as those that attempt to determine in a quantitative way the rate of food consumption, the relationship between availability and selection, the relationship between the quantity of food consumed and its conversion to flesh, and the factors that influence these. Ricker (1946) has discussed much of the literature pertinent to these phases.

Migration and Local Movements

The extent of migration and daily movement may be determined by observing the changes in the pattern of distribution; by observing the fish as they pass falls or other obstacles; by capturing the fish with strategically placed barriers as traps, weirs, and gill nets with due attention paid to time and the direction of movement; by detecting the fish as they intercept a light beam to a photoelectric cell (Hasler and Bardach 1949); and by following the fish by means of the marking-and-recapture technique. The extent of the dispersal of individuals is ordinarily determined by the last method. Since much of the dispersal is accomplished by the young, special types of traps must be used for their capture. Brett (1948) and Wolf (1951) describe traps suitable for the capture of the young.

Reproduction

The sex and state of maturity are better determined from an examination of the gonads rather than from the secondary sex characters which are not invariable. With practice on the larger specimens and by working back into the smaller sizes, one can learn to distinguish the sexes at relatively small sizes. In addition to the categories, adult and juvenile or immature, a third class, subadult, is sometimes convenient. During the approximate season of spawning, adults are commonly divided into three categories; ripe, those individuals that are ready to spawn; green, those that are not yet ready to spawn; and spent, those that have completed spawning.

The number of ova produced by a female during a spawning season is usually determined by direct count of the developed ovarian eggs if the numbers are small and by a sampling technique if the numbers are large. The usual method of sampling consists of relating the number of eggs in a known fraction of the ovary to that of the entire ovary by simple proportion. The size of the sample, relative to that of the whole, is determined either volumetrically or gravimetrically. Applegate (1950) found little difference in accuracy between the two methods, but used the gravimetric method as being more rapid. Katz and Erickson (1950) used dry instead of wet weight in a variation of the gravimetric procedure. Vladykov and Legendre (1940) suggest another technique which seems to be a modification of the von Bayer (1910) method so widely used in fish hatcheries. The determinations are most readily made just prior to the spawning season when the eggs are largest and before any have been deposited.

Age and Growth

Ichthyologists are fortunate in having at their disposal for the study of age and growth a variety of techniques. These fall into three groups: those that involve the use of length-frequency distributions; those that involve the use of specimens of known age; and those that utilize the lines of growth such are are found in many of the hard parts. None of the methods is infallible. Length-frequency distributions are employed to trace the growth of the young during their first season and are also used to analyze the age composition of a

population. Because of the great amount of overlap in size between the older age groups this method is usually not effective in separating more than the first two or three year classes. The growth of fish of known age is followed either in captivity or in the wild. Fish grown in the wild are either marked to make later recognition possible, or else they are planted in waters free of the species. Some doubt exists as to how closely growth under these conditions approximates that under normal wild conditions (Van Oosten 1941). Lines of growth, found in many of the hard parts of the fish, provide the bases for most age and growth studies. The structures most frequently employed for this purpose include scales, otoliths, opercles, dentaries, vertebrae, and fin elements. Various other portions of the skull and pectoral girdle have also been used. Scales are the most convenient and widely utilized.

The convenience of the scale method arises from the ease with which the scales may ordinarily be obtained and prepared for study. Scales commonly are removed from the fish and stored dry until needed, when they are cleansed and then mounted in one of several media. They are examined either with an ordinary microscope or with one of several types of microprojectors such as those described by Van Oosten, Deason, and Jobes (1934) and Mosher (1950). The markings of the thicker and more opaque types of scales are more readily observed in plastic impressions than in the original. The plastic cast is used in the same manner as a scale. A review of the methods of scale preparation is contained in Arnold (1951). Otoliths, fin elements, and other bony parts are used when the scales are absent or unsatisfactory. They are subject to the same limitations as scales, and are usually more difficult to collect and prepare. Sectioning and clearing are commonly required. A microscope with reflected or transmitted light is ordinarily used for examination. The use of bones other than otoliths is discussed by Menon (1950).

The growth history of the individual fish can often be determined from the structures used for the assessment of age since there commonly exists a definite relationship between the growth of these parts and that of the fish as a whole. If this relationship and the size of the fish at capture are known, the length of the fish at any given annulus can be computed from appropriate measurements of the part. If the relationship between length and weight is known, growth in weight may also be determined as was done by Deason and Hile (1947). The relationship between the growth along a diameter or radius of the scale or other part and that of the fish as a whole may be rectilinear or may be more complex; it may remain nearly constant throughout life, or it may change at maturity or at some other time. The most recent summary of the mathematical treatments is contained in Lagler (1952). The problems and mechanics involved are discussed by Schuck (1949).

The labor involved in age and growth studies is often considerable and various ways of reducing the amount have been developed. Ketchen (1950) has suggested making stratified subsamples when the original samples are very large. Specially constructed tables and nomographs (Hile 1950, Lowry 1951) are used to reduce the amount of computation necessary in growth studies.

In spite of its widespread and nearly routine use, the scale method contains serious sources of error. The first few annuli are frequently absent from the individual scales. This is usual in scales regenerated following injury. Sometimes the early annuli are missing because the scales were not formed until after one or more seasons of growth had passed. Delayed formation of the scales is most troublesome when part of a year class forms its scales during one growing season and the remainder during the next. The body-scale relationship may vary in closely similar forms, in different populations of the same species, or on different parts of the body (Carlander 1950, and lit. cited). In addition to the errors inherent in the scales, there are errors of interpretation. Confusion is likely to occur during the period of annulus formation because not all individuals form their annuli at the same time. Check marks, often difficult to distinguish from true annuli, frequently occur. Scale reading is largely an art in which Walford and Mosher (1950) found much of the subjective. Van Oosten's (1941) admonition to determine the validity of the use of the method for each form should be heeded. The assumptions inherent in the use of the growth-ring method for the analysis of age and growth, and the criteria for determining the validity of its use, are well discussed in Van Oosten (1929) and Hile (1941).

In connection with age and growth studies, thought should be given to the types of length measurements to be made and the methods of making them. Some workers prefer to use standard, others fork, and still others total length. Measurements of identical name are not necessarily made in an identical fashion. See Royce (1942), Carlander and Smith (1945), Ricker and Merriman (1945), Hile (1948), and Carlander (1950) for discussions of this problem. If comparisons are to be possible between growth studies based on different length measurements, conversion factors must be determined. It is not wise to mix measurements made on living, freshly killed, and preserved specimens unless there are no demonstrable differences or appropriate corrections have been made. Shetter (1936) and others have found a considerable amount of shrinkage to occur in some forms.

Population Studies

A few population studies have been made using aquaria (Breder and Coates 1932, Shoemaker 1947), but most of necessity have been made in larger bodies of water. Reliable estimates of the size and composition of wild populations of fish are at best difficult to obtain, and, according to Mottley (1949), are more difficult to obtain in streams than in other bodies of water. Trends and relative numbers are easier to obtain than are true population figures. While the available techniques are simple in basic theory, they are not so in actual practice, and often leave much to be desired in the way of accuracy. Most of the methods are effective only for certain categories of individuals such as those that are sexually mature, or those that are within a particular size range.

Population estimates are derived from direct counts, from catch statistics, from marking-and-recapture techniques, and by various combinations of these methods. Direct counts of specific stages are made at particular times of the life cycle of stream-running species with the aid of weirs or traps across the migration route. Direct counts of all individuals are attempted in ponds and other small bodies of water and in selected "typical" portions of the habitat that serve as quadrats for the main area. Ordinarily, considerable labor or drastic means of collection are necessary to make these counts, and rarely are all individuals recovered (Carlander and Lewis 1948). The catch per unit effort is sometimes used in those fisheries where reliable data on the catch and fishing effort are available. The most widely used procedures involve some form of the marking-and-re-

capture technique since it is adaptable to many situations and can be made to include large segments of the population without their destruction. The various difficulties that attend this method include: problems of sampling both as regards the size of the sample that is obtainable at reasonable cost, and the adequate randomization of the marked and unmarked individuals; differential availability or catchability of the marked and unmarked specimens; loss of tags or markings; non-recognition of the tags or markings; migration into and out of the area under study; mortality, both natural and through fishing; and recruitment. For an introduction to the specific techniques and to the basic assumptions, advantages, disadvantages, and limitations that attend the use of these techniques, the reader is referred to the following papers and their chief references: Ricker (1948), Mottley (1949), Adams (1951), Schaefer (1951), DeLury (1951), and Rounsefell and Everhart (1953).

Mortality and Survival

While some of the causes of mortality are often readily identified by observation in the field, their rates and significance can be measured only with difficulty and for a segment of the life cycle. The most generally used methods of study involve the use of marked specimens and age-frequency (catch) curves. The reader is referred to Ricker (1948) and the literature cited therein for a discussion of this problem. Methods of more restricted scope may sometimes be developed by making use of peculiarities of the life cycle of the form under study as for example Murphy's (1952) determination of mortality in the salmon on the basis of the percentage of precocious (grilsing) males represented in the spawning runs.

Outline

Taxonomy

Synonymy; common names; number and description of subspecies; extent of tendency to form local races within the subspecies. Variability; influence of race; temperature, rate of growth, and other factors upon structural features; nature, extent, and probable causes of character clines, if present.

Distribution: Range

General distribution. In terms of political divisions, drainage basins, physiographic regions and barriers, geologic formations or soil types, general climatic conditions, and altitude.

Changes that have occurred in the distribution: through ancient water connections, through physiographic changes, through the agency of man, or otherwise.

Relation of the range to that of cognate forms, and to that of ecological equivalents, *i.e.,* vicarious forms. Areas of intergradation.

Distribution: Habitat

General. Type and size of the body of water usually inhabited; region or major physical habitat usually occupied. Nature of the biotic environment; characteristic stage or stages of succession usually occupied; common plant and animal associates and their relative abundance; indicator species, either plant or animal, of suitable or unsuitable conditions. Role of the species in the community, and its effect upon the environment. Degree of adaptability or tolerance of unusual types of habitat. Variations in the preceding and different portions of the range.

Temperature. Usual range of temperature preferred or tolerated; effect of other features of the environment upon the temperatures that are preferred or tolerated, of time, and of the previous exposure, age, size, and stage of development of the individuals. Effect of temperature on the initiation and rate of various activities such as spawning, incubation, feeding, growth, hibernation, etc. Effects of sudden changes and extremes of temperature; ways of avoiding extreme temperatures and temperature fluctuations.

Current or wave action. Amount of current or wave action that is preferred or tolerated, and the changes that occur with the stage of development and with activities such as spawning, feeding, or resting. Special responses or structional adaptations associated with current such as the degree of streamlining, the reduction of the air bladder, or the occupation of sheltered niches except for short forays into the current.

Depth. Usual and extreme depths occupied, and the normal variation with the stage of development and with type of activities. Relation of changes in depth to the time of day, the seasons, the weather, and the temperature and gas content of the water.

Color of water. Effect of humic or other compounds that may tint the water.

Light. Normal degree of daytime illumination of the habitat; effect of variations in intensity of light upon feeding, spawning or other habits, and upon coloration. Special responses or structural modifications that are associated with the degree of illumination of the habitat such as the relative development of the eyes and other sense organs, and as the development of luminescent organs.

Turbidity. Effect of temporary turbidity upon the daily routine, upon spawning and other seasonal activities, and upon the locus of these activities. Degree of tolerance of permanent turbidity; special habits and characteristics of the sense organs and other structures related to persistent turbidity.

Substratum. Extent of dependence upon, or association with, the bottom or with particular types of bottom for day-to-day existence for special activities, as spawning or for special requirements as shelter. Color pattern and color changes associated with various bottom types.

Shelter. Types of places sought for shelter and the variations with season and stage of development. Modification of the area, or construction, if any. Function of the shelter, as for protection from the current, from enemies, from desiccation, or as places to spawn, or to rest.

Ice. Effects of ice upon the species either directly, or indirectly through effects upon the food organisms, or upon the gaseous relations and other features of the general habitat; variations in the significance of the ice with its duration and with its location as on the surface, in midwater in form of ice crystals (slush), or on the bottom.

Gas content of water. Quantity of oxygen required under ideal conditions, and the minimum that is desirable, and the minimum that can be tolerated for prolonged periods. Environmental factors that influence the amount of oxygen required, as temperature, carbon dioxide, hydrogen-ion concentration, presence or absence of other individuals, and length of exposure. Internal factors that influence the amount of oxygen required as the effect of previous exposure, stage of development, feeding, or other activities. Extent of development of accessory respiratory organs; types of structures involved, and their functional importance as compared with the gills; circumstances under which they are used, as habitually, under condi-

tions of stress, or for temporary descent into oxygen-deficient waters. Quantity of carbon dioxide that can be tolerated and the factors that are influential. Degree of tolerance of hydrogen-sulfide, ammonia, and other gases of decomposition.

Salts. Types and quantities of salts in solution that are required or that can be tolerated; variation in the requirements or limits of tolerance with the stage of development and other factors. Extent of ability to withstand changes in osmotic concentrations and the factors that influence this ability.

Hydrogen ion concentration. Range of hydrogen-ion concentration that is satisfactory, or that can be tolerated; nature of the harmful effects of extremes. Ability to withstand changes in hydrogen-ion concentration. Effect of the hydrogen-ion concentration on the levels of tolerance of other factors.

Pollution. Types and concentrations of pollutants that can be tolerated without detriment; types and concentrations that are detrimental or lethal; factors that influence the levels of tolerance and lethality. Effects of various pollutants upon the organisms and the variations in the toxicity and in effect with the stage of development.

Vegetation. Distribution and abundance of the macroscopic vegetation in the habitat and its relation to food, shelter, and other requirements.

Food. Types and abundance. (See *Food and Feeding* under *Behavior.*)

Competitors. Types and abundance of competitors for items in short supply such as spawning areas, food, or shelter. Competitors, or associates, that are important through their effect upon the environment as, for example, rough fish that may increase the turbidity and thus reduce the vegetation and food supply. Structures, habits, limits of tolerance, or circumstances that favor one or the other of the competing forms.

Predators. Kinds of predator, vertebrate or invertebrate, terrestrial or aquatic, and the stages upon which they prey. Factors that influence losses to predators as: the relative abundance of predator and prey; the availability of buffer species; the abundance of shelter; cryptic structure, hue, or color pattern; weapons such as spines, poisons, electricity, or other noxious qualities; and escape reactions as freezing, swelling, flight, self-burial, aposematic displays, and the assumption of peculiar positions. Nature of the stimuli that produce defense reactions whether produced by the enemy directly, or indirectly through the physical, or chemical, responses of other fish. Variations in the defense reactions toward different enemies with age, size, and physiological state. Effectiveness of the various protective structures and responses against particular predators. Significance of predation in controlling the density, size composition, and well-being of the population.

Parasites and diseases. Kinds of parasites and diseases and the stage, or stages, upon which they prey. Stage, or stages, of the parasite that inhabit the host. Modes of infection; vectors and factors involved. Usual intensity of the individual infections and of the population as a whole. Factors that influence the degree of infection, as the density of the population; the age of the individual and its general state of well-being; the abundance of reservoir hosts, the abundance of vectors, and the season. Effect of the parasite upon the reactions, growth, and welfare of the individual; upon the density of the population; and upon the economic value or desirability of the infected individuals.

Behavior

Sense organs and general responses. Types of sense organs present, their distribution upon the body and their specializations or peculiarities related to a particular habitat or mode of life. Changes in the structure and relative importance of the several sense organs during the life cycle. Reactions to stimuli as: light, both intensity and change; extremes of temperature and temperature change; contact; vibrations; changes in hydrostatic or barometric pressures; current; storms; turbidity; oxygen deficiency; carbon dioxide and other chemicals both those that are normally found in the environment and those, such as specific polluants, that are not; hydrogen-ion concentration; moving objects that might represent either potential enemies or prey; individuals of same or other species that are neither dangerous, nor edible; parasites. Changes or variations in the reactions that occur with the age, size, sex, stage of development, physiological state, and the number of associates.

Evidences of individuality, alertness, curiosity, intelligence, memory, pugnaciousness, vitality, endurance, tenacity of life, playfulness, or group behavior.

Modes of communication, as by the speed and manner of locomotion, by contact, by sound, by light, by chemicals, or by particular movements or positions of the fins, operculum, or other parts of the body. Function of the signals as threats to rivals or enemies, or as a means of species or sex recognition, or as a warning of danger.

Attitudes and locomotion. Characteristic poses or positions assumed when resting, feeding, hibernating, aestivating, threatening, or when alarmed. Mode or modes of locomotion as swimming, leaping, "flying," creeping, darting, burrowing, drifting, or attachment to moving objects. Special peculiarities of locomotion, as the ability to travel overland, or to progress in unusual positions. Speed that can be attained for short distances and that which can be sustained. Functions and relative importance of the body, the various fins, and the exhalatory current in providing propulsive power, in turning, in braking, or in other movements. Structural modifications related to the method of locomotion, as the extent of streamlining; the use of the air-bladder as a hydrostatic organ; the size, shape, and position of the fins; and the possession of special structures such as suckers or holdfast organs. Special larval or juvenile structures and methods of locomotion.

Periods of activity and rest. Usual daily rhythm of activity and rest and the modifications that occur with the seasons, weather, temperature or temperature change, turbidity, moonlight, tides, stage of development, and physiological state. Seasonal rhythm of activity; relative or actual torpidity during summer, winter, or drought; dates and stimuli for entrance and emergence; effect of weather upon seasonal activities.

Food and feeding. Types or kinds of food that are eaten and the relative importance of each type. Source of the food as regards both the general type of area and the particular zones or regions within that area. Dependance upon, or association with other species, as parasites, inquilines, or opportunists. Role of the several sense organs in the discovery of food. Method of capturing food as by active pursuit, watchful waiting, enticement, stalking, gleaning, scraping, straining, or shooting as in the case of the archer fish. Evidence of preference for certain types or the avoidance of others whether obviously obnoxious or not. Extent of mastication. Manner of swallowing; injuries or deaths caused

by prey or by attempts to swallow too large an object. Quantity of food that is eaten during a given feeding period. Usual time and frequency of feeding. Extent of abstentions from food; their causes, their duration, and their effect upon the condition of the fish. Quantity of food required to maintain body weight, to produce a unit increase in weight, and the factors that influence this. Structural adaptations related to the mode of obtaining or of handling food as the general appearance, shape, texture, color and color pattern of the body and modifications of the jaws, teeth, gill rakers, fins, digestive tract and other structures. Variations in the food and feeding habits with: availability; season, individual habit or preference; age; size; sex; physiological state as the advent of reproduction; light, whether daylight or moonlight; tides; turbidity; temperature and temperature changes.

Movements. Nature of the local or daily movements; direction of the movements as from pools to the riffles, or from the depths to the shallows or to the surface; extent of the tendencies to wander seemingly at random through suitable habitats, or to return to the same feeding or resting places over long periods of time; distances usually travelled during the course of a day; periodicities of the movements with the diel or other cycles. Changes that occur in the pattern of movements with age, physiological state, season, temperature, weather, and with the gas content of the water.

Extent of seasonal movements or migrations; functional reason for the migration, whether for spawning, feeding, or the avoidance of unfavorable temperatures; metamorphoses or changes in structure, appearance, or behavior that are associated with migration. Direction of movement as between the ocean or lake and streams, or between the northern and southern portions of the range, or between the shoals and the depths; types of places sought; routes travelled; extent of homing and the degree to which the various stocks tend to be restricted to particular areas or routes; extent of the mixing of stocks at various stages of the life cycle and its economic and biological significance. Mode of travel, as active locomotion, more are less passive drifting with the current, or attachment to other migrants; amount of dawdling or wandering while en route; types and sizes of obstacles such as falls, bars, or stretches of dry land that can be overcome and the types and sizes that act as complete barriers to further movement; mode of surmounting obstacles. Special dangers or causes of losses during migration. Roles of the several sense organs, memory, and chance in locating the route. Times of departure and arrival and the factors that influence these, as temperature, freshets, size, sex, physiological condition, and race; length of time required for each stage of the journey; length of the stay and activities in each area. Number of times that an individual makes the journey during its life; occurrence of non-migratory or land-locked races; differences in growth and behavior between migrants and non-migrants.

Gregariousness. Extent of schooling, and the composition of the schools as regards the sex, size, and age of the individuals, and the inclusion of other species. Changes in the extent of schooling, or in the composition of the group, with the season or with activities such as spawning or hibernating. Organization of the group; mass behavior; responses to various types of stimuli. Changes in the responses of individuals in schools as compared with similar solitary ones.

Spacing phenomena. Extent of a peck order on the feeding, or other areas; and the factors that influence position in the hierarchy.

Extent of territorial behavior; stage or stages that exhibit territorial behavior; relation of peck order activities to territorial behavior. Nature, location, function, and degree of permanence of the defended area or territory. Size of the area defended, and its relation to the size and vigor of the defender and to the density of the population. Degree to which the area is delimited by "boundary lines" and by the limits of visibility or recognition of intruders. Period of time over which the area is defended; extent of temporary desertions for feeding, or for other reasons; cause of the final desertion of the area as defeat in battle, completion of the function, etc. Species and types of individuals against whom the area is defended, and the means employed.

Fighting. Extent of fighting; the apparent causes of strife as competition for food, for mates, for territory, or for position in a peck order; sexes and stages that fight; mode of fighting, as by biting, butting with the head, or thumping with the tail; relation of the mode of fighting to the possession of special weapons as spines or pearl organs. Viciousness, persistence, and outcome of the battle and the variation with the disparity of size, vigor, and physiological state of the combatants. Aposematic display, or ceremonial behavior, as a prelude to, or as a substitute for combat; its nature; and the circumstances under which it is used.

Reproduction

Nature of the sexes. Usual condition, as separate or hermaphroditic; nature and extent of hermaphroditism whether usual or teratological; whether protandrous, protogynous, or concurrent.

Sex ratio in the young and the changes, if any, with age.

Nature and extent of sexual dimorphism, as differences in the size, shape, and color of the body and its parts; or as the development, or degree of development, of special structures; or as the development of parasitic habit in one sex. Nature and period of development of the copulatory organ, if any. Extent to which the secondary sex characteristics are possessed throughout the year, or only through the breeding season; variation in the degree of development of the secondary sexual characteristics with the race, the size of the body, the vigor of the individual, and the condition of the gonads. Functions or uses of the secondary sexual characteristics as: means of recognition; as weapons; as copulatory organs; as holdfast devices for the maintenance of position during mating; as aids in the preparation of the spawning area; or as aids for the placement, retention, aeration, or cleansing of the eggs.

Fecundity. Number of eggs or young produced per egg complement or brood; portion of the body weight represented by the eggs or young; extent of the reduction in the number of eggs or young through non-deposition, or (among live-bearers) through prenatal competition within the brood pouch; the number of egg complements or broods produced by an individual during a year, and during a lifetime; frequency of skipped years or seasons. Variation in fecundity with age, size, health or condition, and race. Correlation between the number of ova or young produced and the nature of the environment.

Spawning. Time of day and season of year during which spawning occurs; length of the period of spawning readiness of individuals of each sex, the local populations, and the species as a whole; sequence of spawn-

ing of individuals in a local population; factors that influence the time of breeding, as temperature, runoff, photoperiod, lunar or tidal cycles, race, size, age, latitude, altitude. Relation of the time of breeding to that of cognate forms, and to those of its associates with which the species might hybridize or compete for spawning facilities, for which it might serve as prey, or on which it might be dependent to provide spawning facilities or prey for the young.

Location of the spawning site as to the general habitat, and as to the specific region or microhabitat where the eggs are deposited, or the nest is prepared, as regards: substratum, current or wave action, depth, turbidity, vegetation, shelter, shore or shoals, the proximity of the spawning areas of other individuals of the same species, the proximity of spawning areas of other forms, both those that are congeneric and those that spawn concurrently; variations in the location of the spawning site because of weather, the abundance of spawning individuals, or other factors; functional advantages and disadvantages of the spawning site.

General appearance, size, and shape of the area actually used, and, if surrounded by a territory, of the area defended; relation of the size of the area to the size and vigor of the individual; extent of the preparation, as none, simple clearing, excavation, or construction; additional preparation or modifications made for successive batches of spawn; extent of the use of natural cavities; portion of the diel cycle occupied in preparation; materials used in construction, as stones, vegetation, or secretions; mode of gathering or producing materials; distances from which materials are gathered; structures used in the preparation of the redd; activities involved in the preparation and testing of the redd for size, shape, or other indications of suitability; number and sex of the individuals involved in the preparation; length of time required and the factors that are influential. Relation of nest building to other activities as migration, feeding, fighting, redd stealing, and care of the eggs or young.

Relative numbers and the distribution of the sexes on the spawning bed at any given time; method by which the sexes meet, such as when both sexes wander through the same habitat, or when one sex remains on the spawning area to which the other makes only brief visits; mode of sex recognition, as through distinctive structures, colors, or markings, or through distinctive reactions as the manner of approach, of flight, or of response to displays and approach.

Nature of the mating act; mode of stimulation to the proper state of sexual excitement, as through display, flight and pursuit, bumping, herding, or biting; number of individuals that participate in a single mating act, as one female to one male, one female to two or several males, or several to many of each sex in a spawning group without the occurrence of specific pairing; positions of the bodies, fins, and genital openings of the sexual partners relative to each other and to the nest or substratum before, during, and immediately after the climax; means by which these positions are maintained, as through the interlocking of fins, contact organs, or adhesive disks; length of time and the number of spawning acts for which any particular group remains together, the causes of dissolution of the group; variation in the mating behavior with different individuals, with different types of habitats, with different populations, and with the changes in the density of the population upon the spawning beds.

Relations of the sexes, as monogamy, polygamy, promiscuity; activities of the sexes after and between matings, such as nest repair or nest enlargement, fighting, resting, covering, or other parental care of the eggs.

Functional significance of spawning activities as a means of insuring the approximation of the gametes, or as a means of placing or retaining the gametes within a particular area. Evidence of sexual selection through courtship tactics, fighting, or otherwise. Comparison of the courtship and spawning behavior in general with those of sympatric forms. Means by which reproductive isolation is achieved or maintained.

Hybridization. Frequency of hybridization; list of other species with which hybridization occurs; method of hybrid formation, as by the chance meeting of gametes or as by direct cross-mating of the parents; factors that contribute to the breakdown of reproductive isolation, such as great disparity in the relative densities of the parental populations, or as drastic alteration of the habitat.

Parental care. Extent of parental care beyond the period of fertilization. If on or within the body of the parents, which sex is concerned; structures involved and their modification; special provisions or adaptations for nutrition, excretion, and respiration of the developing young; stage at which young are liberated; number of broods possible from a single copulation through the retention of sperm; prevalence of superfoetation. If not on or within the body of a parent, the place of protection; the sex(es) involved; nature of the care provided, as aeration, cleansing, or protection from predators. Characteristic poses, activities, and structures of the parent related to the care of the offspring; stage at which care is terminated; cause of termination; length of time involved.

Eggs and young. Appearance of the individual water-hardened egg as regards the size, shape, color, opacity, texture, and projections of the vitelline membrane or shell; and of the vitellus, its size, both actual and relative as compared to the vitelline membrane, and its shape, color, and the number and size of the oil globules; degree of buoyancy and adhesiveness of the eggs. Appearance of the egg mass as regards its size and shape, the number and disposition of the eggs in the mass; the number of females or matings represented in any given redd or spawning site; variation in the stages of development among the eggs of a given mass; specializations or peculiarities of the egg mass related to its particular environment. General features of development; length of the incubation period; effect of temperature, egg size, and race on the length of the incubation period; special structures and activities of the developing embryos; mode of hatching or birth.

Characteristic features of structure, body proportions, and color at hatching, or at birth if born alive, and at representative stages of the metamorphosis to the adult condition; special larval or juvenile structures, and their functions and modifications; length of time in the sac fry, larval, and juvenile stages; length of time required for the absorption of the yolk sac and for the development of the scales, fin elements, and other structures; change of habitat associated with stage of development; time of first taking food and the changes in food and feeding habits with development; changes in other habits during development, as schooling and the reactions to the presence of the parents or other fish, moving objects, light, and passing shadows. Special causes of losses of the eggs or young as: non-fertilization, the non-burial of eggs that are normally covered; their destruction by later redd builders; abnormalities or accidents during

development or hatching; smothering because of silting or because of the position of the egg in the egg mass; stranding as a consequence of a falling water level, persistent wind action, or storms; non-escapement of the larvae from the gravel or redd; diseases and parasites such as fungi; predation by insects and other invertebrates, by the parent, by other members of the same species, or members of other species of fish.

Age and Growth

Methods of age and growth determination applicable to the form in question. If the growth ring method of age determination is used, the nature of the markings that indicate annual rings, periods of spawning, and temporary checks in the growth due to relatively brief interruptions of favorable growth conditions; season when annual rings are formed, and the variation within the population and in different populations. Relationship between the growth of the structure used for growth analysis and of the growth of the body as a whole; changes in this relationship with time, or at the onset of maturity; extent and probable cause of "Lee's phenomenon," an apparent change in growth rate.

Age at which sexual maturity is reached and its variation with sex, race or stock, size, and rate of growth. Longevity, average life expectancy of adults; maximum age; variations in the average and maximum longevity with race, sex, spawning, and rate of growth.

Length and weight attained at the end of each year of life and at the time of reaching sexual maturity; annual increments of growth in length and in weight; length of the growing season; relationship between length and weight; magnitude of the condition factor; variations in the rate of growth and condition factor with age, size, sex, the onset of maturity, previous rate of growth, spawning, and such individual habits as cannibalism, and with race, season, year, population density, and the food supply, temperature, and general nature of the environment.

Mortality

Rates of morality at different stages of the life cycle and the variation with sex and rate of growth. Relative importance of death losses at various stages of life cycle, due to predation, cannibalism, disease, parasites, physiological wear and tear, spawning, and such accidents as choking on prey; winterkill, whether due to reduced temperature or to extreme chemical conditions; summer kill; and the activities of man, as through pollution or through exploitation.

Population Studies

Number and weight of the individuals per unit area; extent of trends and fluctuations and the factors that determine their direction and size; rapidity of recovery from unusual population densities. Composition of the population as regards the age, size, and state of maturity of the individuals; occurrence of dominant year classes. Effect of variations in the density and composition of the population upon the growth of the individual, upon the growth and economic desirability of the population, and upon the environment.

Injuries and abnormalities. Nature, prevalence and causes of injuries or abnormalities as: malformations that result from pollution or unusual environmental conditions; mutilation such as missing maxillaries resulting from angling; injuries sustained during floods, migration or spawning. Extent of ability to regenerate. Effect upon survival, growth, and reproduction.

Economic Value

Ways in which species is actually or potentially of significance to man's welfare, for example: as sources of food, oil, fertilizer, or other valuable products; as a means of pest control; as vectors for parasites of man or animals of signicance to man; as competitors or predators of some more valuable form; or as a source of danger; extent of economic significance. Methods of harvesting and their relative efficiency. Sentiment regarding control; kinds and effectiveness of various measures for increasing and decreasing numbers.

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THE ORDER OF ATTRACTION OF *DROSOPHILA* SPECIES TO CUT PALM TREES

Tropical forests are rich in morphologically similar sibling species of Drosophila. Since such species are often attracted to the same bait, one might think that they occupy the same ecological niches and compete with each other for food. Such competition should, theoretically, lead to eventual elimination of the weaker competitors. On the other hand, closely related species may coexist indefinitely if they differ in their ecological preferences, and natural selection may be expected to favor such a differentiation of preferences. This is indeed what is suggested by the results of Wagner (1944, 1949), da Cunha (1951), and da Cunha, Dobzhansky, and Sokoloff (1951). These authors found that different Drosophila species prefer different species of bacteria, yeasts, and molds as food. Similar conclusions are suggested also by the observations of Hadorn, Burla, Gloor, and Ernst (1952), of Dobzhansky, and Pavan (1950), and Pavan (1952) on the behavior of the adult Drosophila in their natural habitats.

The present author (Burla, 1954) has made collections of Drosophila in tropical forests of the Ivory Coast, in Africa, in 1951. During this work, it has been noted that many species of Drosophila are attracted to the trunks of palm trees belonging to the genus *Raphia* which are cut by the natives for preparation of the palm wine. The sap is collected into clay pots, where it quickly ferments. Such fermenting sap is surrounded by swarms of *Drosophila*. Fermented palm wine proved however to be poor bait when exposed elsewhere in the forest. The species of *Drosophila* attracted to the cut palms belong mainly to the subgenus *Pholadoris*, which is richly represented in Africa and contains many sibling species. The subgenera *Sophophora* and *Drosophila*, as well as the genera *Zaprionus*, *Chymomyza*, *Neotanygastrella*, and *Oxystyloptera* are represented by fewer sepcies. The purpose of the present article is to report observations which indicate that different species of *Drosophila* are attracted to the cut palms at different times after the cutting, and thus display a behavior suggesting that they occupy different, although related, ecological niches.

Material and Method

The observations have been made in a dense primary forest of mesophile character, extending along the eastern boundary of the Ivory Coast. On September 10th, 1951, four palm trees were cut not far from a road leading to the river Comoé. Three of these trees were about 5 meters apart, while the fourth was some 100 meters away. Narrow paths were cut to give access to the cut trunks through otherwise impenetrable vegetation. All four trees belonged to the same species of *Raphia*, and were of approximately the same height and width. Collections of *Drosophila* were made on the evening of the day when the trees were cut, and also on the mornings and evenings of the succeeding days, as shown in Figure 1. The collections were performed by sweeping with a collecting net over the stumps, between 6 and 7 a.m. and between 6 and 7 p.m. Every time the flies were classified, and the numbers of each species were recorded. Weather was nearly uniform during the period of observation, with temperature close to 25° C and some precipitation during the afternoon.

The Data

A total of 5264 flies belonging to 31 species were collected. The records for the ten commonest species are summarized in the histograms in Figure 1. The heights of the columns symbolize the percentages of the total catch of each species found in each collection. The percentages are indicated to the right of the columns.

In agreement with the findings of Pavan, Dobzhansky, and Burla (1950) made in Brazil, and of Hadorn, Burla, Gloor, and Ernst (1952) made in Europe, some species were more abundant in the morning collections, and

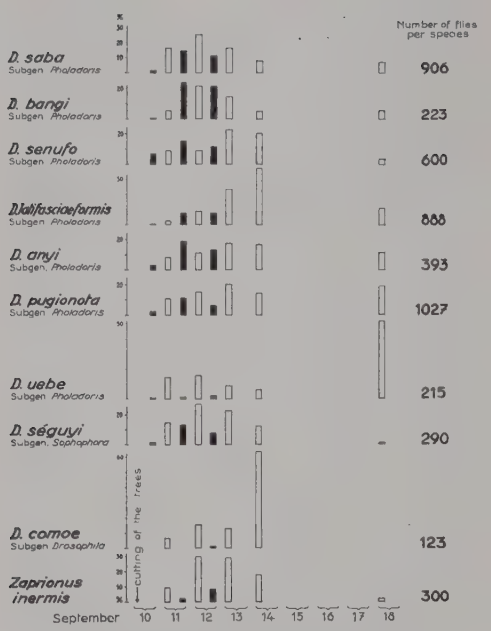

FIG. 1. Proportions of flies of different species collected on different days following the cutting of the trees. The figures on the right indicate the total numbers of the flies of each species collected, those on the left the percentages of the flies in each collection symbolized by the heights of the columns in the diagram. White bars represent flies collected in the morning, and black bars flies collected in the evening.

others in the evening. To the former group belong *Drosophila saba, D. seguyi, D. comoe, D. pugionota, D. uebe,* and *Zaprionus inermis,* and to the latter *D. bangi* and probably *D. anyi.* This differentiated diurnal behavior is pronounced especially in *D. comoe* and *D. uebe.* The other three species showed no clear preference either for morning or for evening activity.

Perhaps more important is the fact that some of the species were most numerous in the collections made on the second and the third days after cutting the trees, and became less numerous in later collections. Other species showed maximum frequencies on the fourth or fifth days. Finally, *D. uebe* reached its peak in the last collection. The early visitors are particularly *D. saba* and *D. seguyi. Zaprionus inermis, D. latifasciaeformis,* and *D. comoe* come later, and *D. uebe* still later. The collection made twenty days after cutting the trees in another part of the forest yielded 114 specimens of *Drosophila,* of which *D. uebe* was represented by 94, *D. bangi* by 9, *D. framire* by 5, *D. saba* by 4, and *D. pugionota* by 2 specimens. At this time the cut surface of the tree was covered with a compact layer of fungi and mosses. It is interesting to note that all five species found at this time belonged to the subgenus *Pholadoris.*

Discussion

Taken as a whole, the data show that the swarms of drosophilid flies attracted to the cut palm trunks changed in composition from day to day during the period of observation. Various species supplant each other as feeders on this particular food source. The visitors arrive in a definite sequence. Obviously, this sequence need not hold true on other types of food, nor for that matter on cut *Raphia* trunks in different geographic regions or under different seasonal weather conditions. The behavior pattern of each species is influenced presumably by a large number of environmental agents, most of which are still unknown. It is a matter of conjecture just what makes some species come earlier than others to cut palm trunks. The composition of the bait obviously undergoes changes, so that the microorganisms which live in the fermenting sap are not the same at different times. The medium in which they live changes also, owing to accumulation of the products of fermentation and of the metabolic products of the visitors.

The fact that each *Drosophila* species shows its own pattern of activity on the cut palm trunks agrees however with the hypothesis that these species, even very closely related ones, are ecologically differentiated. To be sure, the visiting times of the different species overlap broadly (Fig. 1), so that the ecological separation is by no means complete. The different species have still ample chance to compete for food, as well as to hybridize if they are genetically capable of doing so. However, natural selection may be expected only to limit, and not to eliminate entirely, the utilization of the same ecological niche by more than a single species. Excessive specialization might not only expose the *Drosophila* species to risk of extinction, but might also leave many ecological niches in the general environment unoccupied. There must exist a certain balance between interspecific competition on one side and excessive specialization on the other.

Acknowledgments

The data presented in the article were collected during a voyage supported by the Karl Hescheler Stiftung, according to the proposal of Professor E. Hadorn, of the University of Zurich, Switzerland. The analysis of the data was carried out while working on a grant provided by the Brazilian Centro Nacional de Pesquisa to the Centro de Genetica, Faculdade Nacional de Filosofia, Rio de Janeiro. I am indebted to Professor Theodosius Dobzhansky for help with the manuscript.

Summary

Thirty-one species of drosophilid flies were collected on cut trunks of palm trees (*Raphia* sp.) in forests of the Ivory Coast, Africa. Collections were made at different times after the cutting of the trees. Some species were observed to visit the bait chiefly in the morning, and others chiefly during the evening hours. Some species showed a sharp peak of the frequencies, while others were distributed relatively more evenly. Some of the species were attracted very soon after the trees were cut, while other species became frequent only some days later. It is believed that the main reason for the latter finding is the gradual alteration of the bait owing to different stages of fermentation.

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SOME PLANT ACCUMULATORS OF THE MICRONUTRIENT ELEMENTS

The ability of certain species to accumulate relatively large quantities of mineral elements in their tissues has been reported for such elements as selenium (Miller and Byers 1937) and for some of the rare earths (Robinson, Whetstone, and Scribner 1938). Smaller differences in the concentration of cobalt, copper, manganese, iron (Beeson, Gray, and Adams 1947, Beeson and MacDonald 1951) and molybdenum (Robinson and Edgington 1954) have been reported as being characteristic for certain plant species, and environmental circumstances. One importance of such plants lies in their usefulness in evaluating the micronutrient element status of soils.

As part of a comprehensive study of micronutrient elements in Atlantic Coastal Plain soils and forage crops, four commonly browsed plants and a grass were sampled at three periods in each of two years. The sampling was done on six carefully selected sites typical of certain soils in the region.[1] The plants sampled were labeled and subsequent sampling in both years was done on these same plants. Five samples of each species were taken at each sampling period from each site. The details and results of the larger experiment will be reported later.

An unexpected result of the study was the extremely high concentration of cobalt (Table I) found in the leaves of the swamp blackgum (*Nyssa sylvatica* Marsh. var. *biflora* (Walt.) Sarg.). Whereas the cobalt concentration in other plant tissues from these plots ranged from 0.01 ppm to 0.25 ppm (moisture-free basis), no sample of blackgum leaves examined contained less than 0.70 ppm. The highest concentration found in this plant on these plots was 58.9 ppm of cobalt. Subsequent analysis of the leaves of this species were made on samples gathered from Ithaca, New York, and from several locations in Eastern North Carolina and Georgia. The quantities found ranged from a low of 0.25 ppm of cobalt in a known cobalt-deficient region in the Coastal Plain to 118 ppm of cobalt in a sample from Georgia.

Clear evidence was also obtained (Table I) that gallberry (*Ilex glabra* (L.) Gray) accumulates large quantities of zinc, although the differences with respect to other species studied are not as striking as in the case of cobalt in blackgum. The concentration of zinc in the leaves and current year's stems ranged from 18.2 ppm. to 83.0 ppm (moisture-free basis). From the same plots, in broomsedge (*Andropogon glomeratus* (Walt.) BSP.) and blackgum leaves, the concentration ranged from 7.3 ppm zinc to 26.2 ppm.

Blackgum leaves accumlated about double the concentration of copper found in broomsedge, but about the same concentration as found in the leaves of sweetbay (*Magnolia virginiana* L.). Blackgum also accu-

[1] The soil types were examined and identified by A. H. Hasty and G. H. Robinson of the Soil Conservation Service, U.S.D.A.

TABLE I. *Mean concentrations of micronutrient elements found in leaves of five species growing on some typical Coastal Plain soils, season of 1952, three collection dates, five samples per site*

Soil type*	Black-gum	Sweet bay	Gall-berry	Broom-sedge	Pepper-bush
	Co - ppm in dry matter				
Onslow fine sand (1)	1.5	0.02	0.03	0.02	—
Onslow fine sand (2)	3.1	.03	.04	.03	3.0
Bladen fine sandy loam	7.7	.04	.07	.07	9.3
Bladen loam	25.1	—	.09	.08	—
Rains fine sandy loam	26.1	.05	.12	.09	—
Coxville silt loam	30.7	.07	.07	.07	—
	Zn - ppm in dry matter				
Bladen loam	12.5	—	26.5	11.9	—
Coxville silt loam	14.9	15.8	29.5	15.6	—
Onslow fine sand (1)	12.8	15.5	39.1	11.0	—
Onslow fine sand (2)	13.9	11.8	42.5	11.5	81.1
Rains fine sandy loam	11.9	13.0	45.4	14.5	—
Bladen fine sandy loam	13.5	18.6	61.5	13.6	127.5
	Cu - ppm in dry matter				
Onslow fine sand (2)	7.2	7.0	3.8	4.7	6.1
Bladen fine sandy loam	7.1	8.8	4.6	4.8	7.8
Rains fine sandy loam	10.8	9.3	5.2	4.7	—
Coxville silt loam	12.9	9.7	5.7	5.2	—
Onslow fine sand (1)	7.2	11.8	4.9	4.8	—
Bladen loam	12.6	—	5.6	5.2	—
	Mn - ppm in dry matter				
Onslow fine sand (1)	182	86	146	61	—
Coxville silt loam	193	150	176	57	—
Onslow fine sand (2)	236	100	177	61	369
Bladen loam	323	—	187	52	—
Bladen fine sandy loam	154	207	211	63	540
Rains fine sandy loam	578	244	328	130	—

*The soils in each group are ranked according to the specific micronutrient element content of the species examined. In cases of disagreement among species, the best estimate from a consideration of all species was used.

mulated larger quantities of calcium and manganese than did the other species collected.

Pepperbush (*Clethra alnifolia* L.) collected in only two locations in one year, also showed an unusual ability to accumulate cobalt, manganese, zinc and calcium. The leaves of this species contained more zinc than gallberry leaves and a quantity of cobalt equal to that found in blackgum.

The widespread occurrence of both blackgum and gallberry on uncultivated sites should contribute to their value as indicators of the cobalt and zinc status, respectively, of Coastal Plain soils.

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LADYBIRD BEETLES AND ARMY CUTWORM ADULTS AS FOOD FOR GRIZZLY BEARS IN MONTANA

This report describes and briefly discusses two instances of the use of insects as food by grizzly bears. The first involves the phenomenon of mountain aggregations of ladybird beetles. The second represents a clue to the adult behaviour of the economically important army cutworm, *Chorizagrotis auxiliaris* Grt.

Aggregations of overwintering ladybirds (Coleoptera: Coccinellidae) are known to occur in many parts of the world (Balduf 1935). Mountain and ridge tops are frequently sites of these aggregations although the beetles also gather below such points and even in valleys and plains. In western Montana, careful search during summer months under rocks on the tops of high peaks has invariably yielded scattered masses of dozens or hundreds of dead beetles, showing that past gatherings have occurred there. Specimens taken alive from several high ridge and summit areas have been identified by the Unit of Systematic Entomology, Entomology Division, Ottawa, as follows:

Coccinella nivicola monticola Mulsant; 8 August 1952, Squaw Peak, Huson; *C. transversoguttata quinquenotata* Kirby; 4 October 1952, Holland Lookout, Seeley Lake; *Hippodamia caseyi* Johnson; 28 June 1952, 8 August 1952, Squaw Peak, Huson; 20 September 1952, McDonald Peak, St. Ignatius; 16 May 1953, Lolo Peak, Lolo; *H. oregonensis oregonensis* Crotch: 4 October 1952, Holland Lookout, Seeley Lake.

McDonald Peak, in the Mission Mountains, is over 10,000 feet high. The peak and its vicinity are known locally to be frequented by grizzly bears (*Ursus horribilis*) during summer months. The abundance of these bears was the subject of considerable comment by Underhill and Underhill (1950). Two of us have independently observed grizzlies feeding on ladybird aggregations in rock slide areas near the peak.

On August 3, 1932, while climbing McDonald Peak, a group of twelve grizzly bears was encounered (by J.R.) in a high rocky basin, just below the summit. The bears were watched for several minutes and were seen to be overturning rocks and apparently feeding. After they had been disturbed and had left the area the site of their activity was examined. Ladybird beetles were present in large numbers under and among the rocks there. Snow banks were still abundant and the beetles apparently represented overwintering aggregations.

Since that time a number of trips have been made into the Mission Mountains in order to observe the bears. They have been seen on numerous occasions and moving pictures have been made of them near McDonald Peak. Some of the pictures show these animals on rock slide areas, moving rocks and apparently seeking food. Such behaviour might be associated with search for rodents; however, this is not likely in view of the site, the known presence of ladybird masses in the general area, and the previous observations on the bears.

Another of us (J.S.), in the summer of 1932, saw grizzly bears frequenting rock slides where ladybirds were abundant. These insects were of particular interest at that time because it was known that in certain parts of the country they were being collected and sold for release in orchards, as a means of controlling aphids and other insects. A resident of the Swan Valley, east of McDonald Peak, had reported seeing grizzly bears rolling rocks on the slopes of this peak and eating the ladybirds which they found in this way. The area was visited in order to collect samples of the beetles and to determine whether or not it would be possible to gather sufficient numbers of them to sell. At that time some of the bears were encountered above timberline on the east slope of the peak and were seen to be overturning rocks and apparently feeding. After they had moved away large masses of ladybirds were found beneath every good-sized

rock in the area. It was estimated that some five to ten gallons of beetles could be collected per day in the vicinity. The species was not one of those in demand, however, and no further visits to the area were made.

There is little doubt that in each of these cases the bears were actually feeding on ladybird beetles when first seen. This appears to be the first reported instance of such predation on aggregations of these insects.

After hearing of the above observations an attempt was made (by J.C.) to determine whether or not there was any current use of these insects as food by the bears. This attempt led to an unexpected and interesting finding. On Sept. 19 and 20, 1952, a visit was made to McDonald Peak and vicinity and portions of all bear droppings found were collected. Fifteen samples were taken, mostly between 8,000 and 9,000 feet, where groups of timberline trees were scattered among rock ledges and grassy areas. All droppings were estimated to be a month or more old when found. In view of their locations and the known past occurrence of grizzly bears in the area it is safe to assume that they came from grizzlies, not black bears.

Microscopic examination of the samples revealed that nine of them consisted largely or entirely of moth remains. It was quite apparent, moreover, that only one species, or group of closely related species, was involved. No ladybird remains were seen in any of the samples and a few ant and midge parts comprised the only other insect material. Grass, sedge and shrub remnants, pine nut hulls, hairs and traces of soil made up the non-insect portions. By reconstructing the male genitalia, T. N. Freeman, Systematic Entomology Unit, Entomology Division, Ottawa, was able to identify *Chorizagrotis auxiliaris* Grt., the army cutworm, in the material.

This insect is endemic to the Great Plains and is a species of considerable economic importance in cultivated land areas of the semiarid region of western North America (Strickland 1916; Cook 1927; Seamans 1929; Walkden 1950). An aspect of the life history of this moth has long been puzzling. In a given locality an early summer flight period occurs, during which the females have undeveloped ovaries. This is followed by mid-summer disappearance of the moths. In late summer or early autumn they again appear and fly actively. This time the ovaries are fully developed and oviposition takes place. The second flight period involves smaller numbers of moths and specimens appear worn.

This pattern of flights was first interpreted as indicating two broods a season (Gillette 1904). Later studies have shown that this is not the case. It is usually considered that the moths estivate during the warmest part of the summer. In Alberta, inactive adults have been found in barns and houses, under clods of earth and in a variety of protected places, and are reported to stay in buildings throughout the summer (Seamans 1929). There is evidence, however, that during this time large numbers of the moths are present at higher altitudes, in nearby mountains.

Pepper (1932) reported that in Montana these moths were extremely abundant in outbreak areas early in the season but had completely disappeared by mid-summer. During several evenings in July, essentially unidirectional flight of numbers of them was observed. Pepper speculated on the possibility that they migrated to higher elevations and estivated there. He cited the case of *Agrotis ypsilon,* which shows a similar period of disappearance and is suspected of flying from Egypt to the Alps, or, in India, some 200 miles to the mountains there. Walkden (1950) recorded three observations of numbers of active adults in the mountains of Colorado and Nevada. Pepper later (personal communication, 1954) reported that two reliable observers had seen great numbers of these moths at higher altitudes in Montana. One of us (J.C.), on July 28, 1952, saw numbers of the moths, at dusk, flying about alpine flowers near the summit of Squaw Peak, Huson, Montana. Also, many of them were taken at various times in water pan traps near and at the top of this 8,000 foot peak in connection with other studies (Chapman 1954).

All reports of the moths at higher elevation indicate that they are active there and it is possible that they do not estivate at these elevations. Actually some feeding would be expected in connection with the development of ovaries which is known to take place before their reappearance in lower areas. Presumably, while in the mountains, the moths seek shelter during the daytime and in unfavorable weather under logs and rocks, as they are known to do in the lowlands. Thus, if large numbers of moths were in a mountain locality the bears would be able to find and eat quantities of them. The Mission Mountains border the Mission Valley, which is intensively cultivated, but the army cutworm was not reported to be abundant in this area during the summer of 1952 (Pepper *et al.* 1953).

Grizzly bears, like black bears, are quite omnivorous (Seton 1929; Holzworth 1930; Cooney 1941) and would be expected to eat any insects found in quantity. The feeding of black bears on crickets and grasshoppers in the Yellowstone National Park area was observed by Murie (1937), and Gurney (1953) cites a report of black bears feeding on grasshoppers stranded on mountain snowfields. In these cases also, availability of insects appeared to be the main factor in their selection as food.

We wish to thank T. N. Freeman for identifying the army cutworm and W. G. Wellington for reading the manuscript.

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RELATION OF LIGHT INTENSITY TO BASAL AREA OF SHORTLEAF PINE STANDS IN GEORGIA

It is well-known to foresters that pines will not reestablish under the canopy of pine or pine-hardwood stands in the Piedmont region. There is considerable evidence that low shade of hardwood brush is just as detrimental to pine reproduction as high shade. The pines require overhead sunlight that is high enough in intensity for them to produce the food that is needed for vigorous growth of roots and shoots. The results of recent studies have shown the importance of adequate light intensity in the course of the regeneration of southern pine species.

In 1948, Wahlenberg reported on the effect of forest shade on growth of loblolly pine (*P. taeda* L.) seedlings in southern Arkansas. It was found that on favorable sites a canopy opening with a radius of 7.6 to 15.2 feet or larger was adequate for continuous pine production. This was regarded as the size of opening created by the removal of a single tree. However, the growth was more rapid and survival better in the larger openings. Further evidence of the importance of light is shown by a study that Oosting and Kramer (1946) made of the relation of water and light to shortleaf pine (*P. echinata* Mill.) reproduction in the Piedmont of North Carolina. They concluded that light was probably more controlling than soil moisture in the complex of factors that limit the establishment of shortleaf pine seedlings in forest stands. Brinkman and Swarthout (1942) observed that loblolly pine and shortleaf pine in east-central Alabama did not reproduce unless the overhead space was 50 per cent open in old-field stands or 65 per cent open in natural stands. They concluded that pine reproduction is definitely restricted when the overstory competition leaves less than 40 per cent open space in the canopy. Liming (1946) reported that the height growth of planted shortleaf pine increased progressively as the overhead release in a 40-year old hickory stand increased from zero to 100 per cent. These and other reports indicate that the course of pine reproduction in partially cut mature stands depends on the amount of sunlight that the seedlings receive for growth. Thus, the use of partial cuttings has introduced the need of a method for estimating the amount of cutting needed to get any desired light intensity beneath the canopy. To obtain information on this subject, a study was made of the relation of basal area to light intensity in pure shortleaf pine stands.

METHODS

The data used in the study were taken in pure even-aged shortleaf pine stands located in six counties in the northeastern part of the Georgia Piedmont. For uniformity of results, the only stands selected were those that exhibited no observable evidence of disturbance by cutting, fire, or grazing during the previous ten years. The measurements were taken on a single ¼ acre square plot in each of the widely distributed stands. Diameter outside bark at breast height was taken on all trees on each plot. For calculation purposes, the diameters were arranged in 1-inch classes.

Light intensity at breast height in the understory was measured with a Weston illumination meter (Model 756) which records sunlight in footcandles. A sphere globe of opal glass was attached to the light absorbing unit containing the photoelectric cell. Light measurements were made on clear days between 9:00 a.m. and 3:00 p.m. The average light intensity was obtained from 10 rows of 10 readings made each way on the plot, giving a total of 100 readings. A measurement of full sunlight was made in the open near the stand at the time the plot was measured. For comparative purposes, the average light intensity of each plot was calculated as a percentage of full sunlight.

Age of the stands selected varied from 30 to 100 years. The basal areas of all plots were well-distributed throughout a range of 35 to 163 square feet per acre. Sampling had to be limited to plots with 35 or more square feet of basal area because the relation of light intensity to basal area became increasingly erratic in open stands. Light intensities on all plots ranged from a minimum of 12 per cent to a maximum of 63 per cent of full sunlight.

RESULTS

An analysis of the data taken on 31 plots showed a strong correlation between average percentage of full sunlight and basal area. The logarithmic equation for the basal area-light intensity relationship was solved by the use of the method given by Goulden (1947). The following equation was derived: $\log y = 3.5177 + (-1.0586) \log x$. The corrected light intensity values used for curve shown in Figure 1 were calculated by substituting the basal area values in the equation. The corrected light intensity values are also given in Table I.

A feature of the curve that is of special interest is the manner in which the light intensity varied with basal area above and below 100 square feet. From 100 to 40 square feet the total increase in light intensity was 41 per cent as compared with only 9 per cent from 160 to

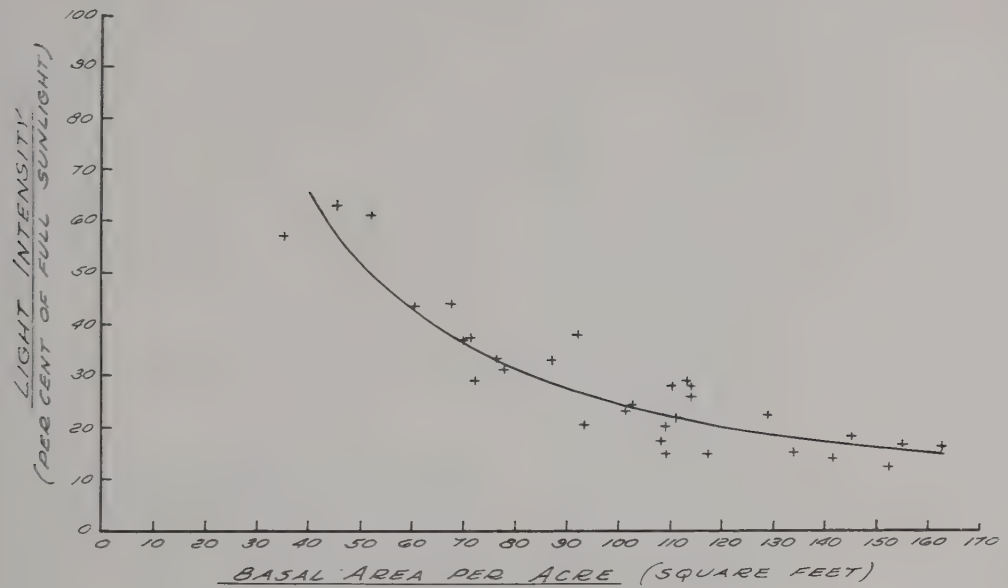

FIG. 1. Relationship between basal area and light intensity in shortleaf pine stands.

TABLE I.—*Relation of corrected light intensity values to basal areas of shortleaf pine stands*

Basal area (Sq. ft.)	*Light intensity* (Per cent)
40	66
50	52
60	44
70	37
80	32
90	28
100	25
110	23
120	21
130	19
140	18
150	17
160	16

100 square feet. These data offer a guide to the amount of cutting needed in pure shortleaf pine stands to get light conditions favorable for pine reproduction. There is need, however, for more research on the marginal light intensity that is necessary for vigorous growth reproduction.

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FOULING ORGANISMS ATTACHED TO THE AMERICAN LOBSTER IN CONNECTICUT WATERS

In Herrick's classic monograph on the American lobster (1895: p. 122) it is pointed out that "the lobster is encumbered with a great variety of messmates, which attach themselves to the external shell." The following types of organisms are mentioned in particular: barnacles, mussels, tunicates, tube-forming annelids, bryozoans, nullipores, hydroids, algae, and fungi.

While engaged in studies on the American lobster (*Homarus americanus*) at the Marine Hatchery of the Connecticut State Board of Fisheries and Game located at Noank, the writer had an opportunity to gather some precise data on this problem. Egg-carrying lobsters brought to the hatchery by the lobstermen are retained in hatching boxes for hatching and rearing of the lobster fry (Dexter 1952). Between June 17-20, 1946, there were 538 of these on hand which were carefully examined

TABLE I. *Fouling organisms on females-in-berry (shell nearly two years old). Total number examined, 538; total with fouling organisms, 425*

Species	No. of Occurrences	Percentage of total	Site of attachment and abundance
Alcyonidium polyoum (Encrusting bryozoan)	326	60	On all surfaces. Less than 1 sq. in., 110; 1 sq. in., 74; 2 sq. in., 80; 3 sq. in., 41; 4 sq. in., 16; 5 sq. in., 4; 6 sq. in., 1.
Balanus crenatus (Barnacle)	100	54	Among teeth of claws, 80 (1-28 on each), on carapace, 7 (1-4 on each); on joints of claws, 7 (1-7 on each); on "hand" of big claws, 5 (1-5 on each); on seminal receptacle, 1.
Anomia simplex and A. aculeata (Jingle shell-bivalves. All but 3 were A. simplex.)	86	16	On claws, 57 (1-7 on each); among teeth of claws, 11 (1-3 on each); on carapace, 8 (1-2 on each); on walking legs, 5; on uropods, 3; on seminal receptacle, 2.
Molgula manhattensis (Tunicate)	70	13	On seminal receptacle, 44; on ventral spines, 25 (1-2 on each); on basal segment of claw, 1.
Mytilus edulis (Blue mussel)	25	4.6	Between exopodite and endopodite of uropods, 20 (1 had 2 mussels); on inner surface of pleura, 2 (1-2 on each); on ventral surface of abdomen, 1; between exopodite and endopodite of pleopod, 1; on seminal receptacle, 1.
Bugula turrita (Arborescent bryozoan)	23	4.2	On ventral spines, 18; on seminal receptacle, 4; on carapace, 1.
Serpulid (Tube-building annelid)	17	3.0	On carapace, 8; on walking legs, 4; on claws, 3; on abdomen, 1, on seminal receptacle, 1.
Crepidula glauca and C. fornicata (Gastropods; gray slipper, 11; boatshell, 2)	10	1.8	On uropods, 5; on claws, 3; on carapace, 1; on telson, 1.
Campanularia flexuosa (Hydroid)	7	1.3	On claws, 3; on carapace, 2; on ventral spines, 1; on walking legs, 1.
Acanthodesia tenuis (Encrusting bryozoan)	3	0.5	
Bowerbankia gracilis (Bryozoan)	1	0.2	
Electra pilosa (Encrusting bryozoan)	1	0.2	
Sponge	1	0.2	On ventral spine, 1.
Anthozoan (Sea anemone)	1	0.2	On pleuron, 1.

for the presence of macroscopic fouling organisms. These lobsters were all females-in-berry and were of legal commercial size. The average weight was 934 grams and the age of each exoskeleton approximately 2 years. A total of 425 (79%) had attached organisms. Of these, 257 had only one species attached; 124 had two species; 38 had three species; and six had four species attached. Table I summarizes the results.

In addition, 198 lobsters taken by trapping in Fisher's Island Sound in the months of July and August, 1946, were examined for fouling organisms. These lobsters had recently moulted and the shells were approximately one to two months old. They were captured in four special traps set in a depth of 16-20 fathoms. They ranged in size from 14.6 to 25.0 cm., the average length being 19.6 cm. The range in weight was 100-521 gm., with an average of 252 gm. Only 52 (26%) contained fouling organisms. Not more than a single species of attached animals was found on any one lobster. Table II summarizes the results. One of the specimens collected contained an anomalous appendage which had grown from the left side of the carapace (Dexter 1954).

TABLE II. *Fouling organisms on new-shell lobsters (shell 1-2 months old). Total number examined, 198; total with fouling organisms, 52*

Species	No. of Occurrences	Percentage of total	Site of attachment and abundance
Alcyonidium polyoum (Encrusting bryozoan)	49	25	On all surfaces. Less than 1 sq. in., 28; 1 sq. in., 13; 2 sq. in., 4; 3 sq. in., 3; 5 sq. in., 1.
Balanus crenatus (Barnacle)	2	1	On carapace, 1; on claw, 1.
Anomia simplex (Jingle shell)	1	0.5	On ventral abdomen.

It will be seen that Bryozoa make up the bulk of fouling organisms on lobsters in Connecticut waters. Next in importance are the barnacles, bivalves, and tunicates. Tube-building annelids, sedentary gastropods, coelenterates, and sponges are of little importance.

Acknowledgment is made to the Bingham Oceanographic Laboratory, Yale University, and the Connecticut State Board of Fisheries and Game, organizations for which the writer served as Temporary Aquatic Biologist in the summers of 1945-46 while carrying on research on the American lobster. Thanks are also due to Louis W. Hutchins, Woods Hole Oceanographic Institution, for making identifications of the Bryozoa collected in this study (Hutchins 1945).

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A BORER FOR SAMPLING IN PERMAFROST

Pollen analysts and soil workers have throughout the years found it difficult or impossible to take samples in permafrost. In regions where permafrost prevails it is also a problem to transport heavy equipment or to use equipment which would not permit sampling at a minimum loss of time. All of these factors occupied the attention of Prof. Albert Courtemanche, director of the Department of Biogeographie at the University of Montreal, and of the writer prior to a long bog sampling trip by plane into the tundra and forest-tundra ecotone regions of northern Quebec during July 1954.

Mr. Courtemanche finally solved the difficulty in a satisfactory manner. His study of problems of making borings in permafrost culminated in the construction of a simple instrument which can take at a single boring a core two inches in length and one inch in diameter (Fig. 1).

FIG. 1. The Courtemanche permafrost borer.

When the borer was first constructed, it was tried out on blocks of ice and frozen peat, prepared in a refrigerator at —10°C. Results were successful and perfect beyond expectation. The instrument is made of hardened steel and weighs about 18 ounces. Since we also carried a Hiller borer, the Courtemanche permafrost borer was made to fit the same rods.

Shortly before leaving on our trip, we visited the Arctic Institute of North America and there found a description of a similar but more complex borer developed by A. M. Pehelincev, a Russian worker, whose instrument is officially called "Core Taker." His instrument has eight cutting teeth, and the inside diameter is one mm wider at the top than at the bottom to facilitate removal of the core. It takes a core 100 mm high by 63 mm wide.

The Courtemanche borer has only two cutting teeth (Fig. 1) and the diameter of the tube is uniformly the same. This makes removal of the core at times difficult. The Courtemanche borer has on two sides two 5/8 inch openings above the sampling section so that the core can be forced out with a screw driver pushing against a packing of sphagnum.

On the trip, the Courtemanche borer gave perfect service. Samples were taken as quickly from permafrost layers as samples of peat with the Hiller borer. The borer also proved itself efficient in taking samples from compacted sandy layers, and even in coarse sand. Borings were made through a maximum depth of six feet of sand, but there is no reason why samples could not be obtained from deeper layers. In the tundra work, we encountered organic sediments alternating with layers of sand, and samples were obtained with ease. At times, the borer brought up cores of solid ice. Borings to a depth of five feet, with samples taken at one-inch intervals, were made approximately in one hour.

If sampling is in part by the Hiller borer (above permafrost layers), the borings with the Courtemanche borer should be made in the same hole. If no such initial boring through soft material has been made, it can be made with the Courtemanche borer before sampling in permafrost or in compacted layers of sand begins. The light weight of the instrument and its simple attachment to the rods of the Hiller borer permits carrying it as regular equipment. Exchange of the borer can easily be made when sandy layers or compacted material is encountered. The inventor will gladly answer any questions relating to the borer.

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SEASONAL ABUNDANCE OF THE TICK *DERMACENTOR PARUMAPERTUS*[1]

The tick, *Dermacentor parumapertus,* which is confined to the arid and semi-arid regions of western United States, has been considered to be of little economic importance. This tick rarely attacks man and for many years has been assumed to be host-specific on the Leporidae. "Stage to stage survival of spotted fever virus has been shown under laboratory conditions and it appears quite probable that within its natural geographical range it [*D. parumapertus*] functions as an agent in the transmission of spotted fever among rabbits" (Parker *et al.* 1937: 60). This tick is a reservoir for tularemia in both rabbit and rodent populations (Woodbury and Parker 1954). Tests performed by personnel of the Rocky Mountain Laboratory show that it also serves as a reservoir for Colorado tick fever (G. M. Kohls, personal communication, 16 Sept. 1953).

A study currently being conducted by one of the coauthors (A.G.) indicates that many species of rodents also serve as hosts for the immature stages of *D. parumapertus.* Hence, this tick may be an important factor in perpetuating and disseminating pathogens within and between rodent and rabbit populations. It was deemed necessary, therefore, to study the seasonal abundance of each developmental stage of *D. parumapertus* in order to understand better this tick's potential ability to transmit microorganisms. The report which follows presents the results of a year's study of the seasonal abundance of *D. parumapertus* as a parasite of the black-tailed jack rabbit, *Lepus californicus.*

This rabbit was used in this study for several reasons. (1) It is known to be susceptible to Rocky Mountain spotted fever, Colorado tick fever and tularemia. (2) It is the common host on which larval, nymphal, and adult stages of *D. parumapertus* are found. (3) It is relatively abundant and available throughout the year. (4) It may be collected easily.

A suitable area with a relatively high rabbit population was selected adjacent to the Great Salt Lake Desert, twelve miles west of the southern end of the Cedar Mountains in Tooele County, Utah. This semi-stabilized sand dune area is three miles long and one-half mile wide. The predominant plants are greasewood (*Sarcobatus vermiculatus*), four-winged salt bush (*Atriplex canescens*), ink weed (*Suaeda torreyana*), shadscale (*Atriplex confertifolia*), rabbit brush (*Chrysothamnus* sp.), sacaton grass (*Sporobolus airoides*), and Indian rice grass (*Oryzopsis hymenoides*). An extensive greasewood and shadscale flat borders the sand dune area.

The annual precipitation in this area is approximately eight inches, more than half of which occurs during March, April, May and June. Mean monthly temperatures of 60° F. occur from May through September. January, the coldest month, exhibits a mean low of 26° F. The temperature extremes recorded in 1953 were 109° F. in July and —15° F. in January. The mean relative humidities ranged from 28.5% in September to 77.9% in January.

The field work for this study was initiated on 1 April 1953 and was continued until 1 April 1954. During this period, five rabbits were collected every seventh day (with minor exceptions). As soon as they were shot, the rabbits were placed in paper bags and the bags were sealed to insure the retention of the parasites. Before subsequent processing was begun in the laboratory, the animals in their containers were refrigerated at —4° F. for two to three hours. This procedure was found to be the most desirable method of immobilizing the ectoparasites. Although not sufficient to freeze the rabbits, this interval of refrigeration slowed down these extremely active ticks and facilitated collection. Unlike gassing and anesthetizing procedures, refrigeration allowed the parasites to remain alive for further studies.

At the end of the refrigerating period, each rabbit was placed in a large, deep collecting pan. The paper bag containers were examined and the detached ticks were collected: those which remained attached to the rabbit were removed with forceps. While held over the pan, the animal was throughly brushed to remove the remaining parasites. To insure a complete collection of the larvae and nymphs, the pan and the accumulated sand and debris were examined under a binocular dissecting microscope. The ticks were preserved in 70% alcohol or were kept alive for further study. *Cuterebra* larvae, fleas, lice and heleid gnats found during the processing were also collected, but are not treated in this report.

Each tick was examined microscopically to determine its species, sex, and stage of development. Records were kept of the numbers of larvae, nymphs and adults which were removed from each host. The weekly average per rabbit for each of these stages is presented in the graphs.

During the course of this investigation, 8180 ticks of the species *D. parumapertus* were collected and examined. The most heavily infested rabbit was collected on May 7 and was found to harbor 447 ticks. Two additional species of ticks were found on the rabbits. One hundred and fifty-nine *Otobius lagophilus* were found on six of the animals and one *Haemaphysalis leporis-palustris* was collected.

Fleas (*Pulex irritans*) were collected from nineteen rabbits. Sucking lice (*Haemodipsus setoni*) were collected from one rabbit, and heleid gnats (*Culicoides* sp.) were found engorged on another. *Cuterebra* larvae were abundant throughout the summer months.

Adults

The adult population of ticks reached its peak in the latter part of July (Fig. 1). This peak is produced by the summation of adults recently molted from nymphs and overwintering adults that had not engorged during the previous season. The adult population was consistently low throughout the rest of the year.

Female ticks were more numerous than males during the period between 29 July and 23 September. The females were engorging at this time in preparation for egg

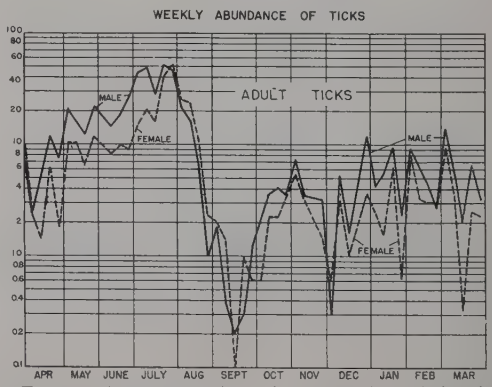

Fig. 1. Average number of adult male and female *Dermacentor parumapertus* ticks per rabbit for each week through one annual cycle.

[1] The authors wish to express their sincere appreciation to the staff of Ecological Research for their assistance in this study.

laying. Except for this relatively brief seven-week period males predominated. Of the total number of adult ticks collected during this study, 59% were males.

Nymphs

The nymphs were most abundant during the moist months of April, May and June (Fig. 2). It may be noted that there is considerable fluctuation in graphs of both nymphs and larvae. The authors feel that these fluctuations would probably smooth out with larger samples. However, the data seem adequate to indicate the general relationships of larvae, nymphs and adults.

Since ticks stand a very poor chance of surviving through the winter in the engorged state (Hooker *et al.* 1912), it seems probable that the spring nymphal population wintered in the unengorged state rather than as engorged larvae. No nymphs were collected between early July and late September 1953. The relatively large number taken during October probably developed from larvae which molted following estivation, and found a host before the onset of cold weather.

Larvae

The larvae, like the nymphs, were most abundant during the spring months (Fig. 2). They appeared suddenly during the latter part of February, and large numbers were collected until the middle of May. Following the spring peak, there was a gradual decrease in numbers until the larvae disappeared completely in the middle of June. A relatively large population appeared again in the early part of October and declined abruptly in the same month. From the 21 October until 25 November, a very small number of larvae were collected each week. A short-lived peak occurred on 2 of December and disappeared completely two weeks later. Larvae were virtually non-existent until 17 February 1954.

It is probable that the spring larval peak results from the hatching of eggs which over-wintered. Moisture is essential to the immature forms, and the complete disappearance of the larvae during the extremely dry summer months indicates a period of estivation.

The October larval peak may be due to (1) those larvae which estivated after failing to find a host the preceding spring, and/or (2) the larvae which hatched from eggs deposited by the females early in the season.

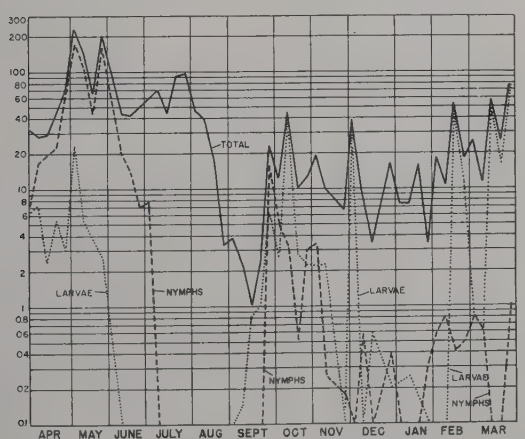

Fig. 2. Average number of nymphs and larvae and the total numbers of all stages of *Dermacentor parumapertus* ticks per rabbit for each week through one annual cycle.

The abrupt peak which occurred in December may be a reflection of hibernating ticks which were reactivated, for a short time, by unseasonably warm weather.

If the tick population trends observed in this study are typical, the following conclusions may be drawn:

(1) *Larval* populations on the jack rabbit are not of sufficient magnitude to maintain the high *nymphal* populations found on these animals.

(2) Larval ticks must frequently use hosts other than the jack rabbit in order to maintain this high nymphal population. The subject of alternate hosts for *D. parumapertus* will be treated in greater detail in a subsequent report.

Summary

An investigation was made of the seasonal abundance of the tick, *Dermacentor parumapertus,* which is parasitic on the black-tailed jack rabbit, *Lepus californicus.* This one-year study was made in a vegetated sand dune area in Tooele County, Utah. Approximately 8300 ectoparasites were collected and identified in addition to the quasi-endoparasitic *Cuterebra* (rabbit botfly) larvae. The six species of ectoparasites represented consisted of three species of ticks, one of fleas, one of sucking lice, and one of heleid gnats. *D. parumapertus* is by far the most abundant ectoparasite found on the jack rabbit.

Ticks of the species *D. parumapertus* were found on jack rabbits throughout the year, but maximum infestation occurred in May. Approximately 75% of this spring population was composed of nymphs. Larvae were also numerous in the spring, but at no time did they reach the proportions of the nymphal population. The adult ticks were most numerous in July.

The relationships of the larval and nymphal populations found on *L. californicus* indicate that *D. parumapertus,* long thought to be host specific to the Leporidae, is parasitic in its larval stage on hosts other than the jack rabbit.

In this region where rodents and rabbits are agricultural pests, *D. parumapertus* may be of considerable economic importance as a vector of the diseases endemic in these populations.

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REVIEWS

Agro-Climatological Classification of Regions[1]

The problem of the establishment of climatic regions on a "realistic" basis has long been one of the major preoccupations of scholars in the several fields where climate is of major consequence. While it is true that from De Candolle onwards plants have been used extensively by climatologists, Dr. Filzer's main criticisms of climatological systems such as those of Köppen are that they do not allow easy and low-cost measurements over large areas, that they restrict measurements to a limited number of individuals that are to reflect the entire climatic "spectrum" of a vegetation association, and that they do not take into account all of the elements of the environment.

Dr. Filzer's agro-climatological approach is somewhat different from those mentioned above. His basis of measurement is agricultural (i.e. limited in its application to areas where detailed agricultural statistics are available). Using Germany as an example, and building his statistical base from production figures and data giving cropland surfaces, he establishes dry equivalents for a series of crops common to the areas under investigation. His method is to establish a series of years as a basis for the correlation data upon which his system is founded. Such a series of years (1926-1937) is subsequently plotted in terms of the dry crop equivalents, 12 given as the maximum index for the highest production year, 1 as the lowest when the series consists of 12 years. The next step is to compare this series of data (e.g. the Merseburg region of north central Germany, where the series reads: 11-8-6-9-7-5-1-2-12-10-4-3-) with a series for the neighboring region (e.g. Magdeburg, where the series reads: 11-10-7-9-6-5-2-1-12-8-4-3). The differences between the two series would be: 0, -2, -1, 0, 1, 0, -1, 1, 0, 2, 0, 0, giving a total of 8 as the "discrepancy value" between the two series. The author then sets up five categories of discrepancy values: 0-8, 10-16, 18-24, 26-32, and above 33. It is his thesis that this figure, the discrepancy value of two adjacent regions, affords a true index of the climatic-edaphic-floristic relationship of the two regions and allows the setting up of realistic climatic zones.

Filzer attempts, with considerable success, to define climatic regions on the basis of production figures, arguing that crop statistics provide a realistic index of the influence of *all* natural factors. In his discussions, he shows rather striking examples of his method applied to climatic zones of transition where the influences of two or more major climatic types are clearly reflected in crop statistics translated into crop series and discrepancy values. Perhaps one criticism should be made at this point, though; the author's method is one of considerable promise where detailed agricultural statistics are readily available for a variety of crops, related to a large number of relatively small districts, and covering a long period of time. But the climatologist, even when dealing with regions of dense settlement and well-developed agriculture cannot always count on the vast array of crop statistics that would seem to be the indispensable prerequisite of the method here described.

It would be interesting to apply the method proposed by Dr. Filzer to Dr. Weaver's investigations of the agricultural geography of the Middle West. (cf. The Geographical Review, April and October, 1954). The results of such an agro-climatological inquiry might very well introduce new ideas into our concepts of American climatic regions.

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[1] Filzer, P. 1951. *Die naturlichen Grundlagen des Pflanzenertrages in Mitteleuropa.* viii + 198 pp. Stuttgart E. Schweizerbart'sche Verlagsbuchhandlung. DM 17.60.

A New Manual of Colorado Plants[1]

The need for a new manual is demonstrated by the statement in this book that one out of every 30 species listed in it is a new record for Colorado. It covers both the Pteridophyta and the Spermatophyta. The keys are especially useful to the ecologist, who must often identify plants in vegetative condition, because they usually contain at least 2 characters. In all, 2794 species have been described and about 350 additional species are included in the keys but actual specimens from the state have not been seen although they have been reported from Colorado or may be expected to be found there. The descriptions are very satisfactory. The data on geographical and altitudinal ranges are definitely helpful in identification. Synonyms and common names are given. No new species and only 18 new combinations are proposed. The author has attempted to bring the nomenclature up to date by following the latest taxonomic treatises. This resulted in unavoidable changes in many old names. The definitions in the glossary are brief but adequate and the index includes both scientific and common names. The lithoprinting process was used in order to reduce the cost to a reasonable figure. The book is in large format, well bound, not too large to use in the field. Typographical errors are rare, such as "glakes" for flakes on p. 175 and "peals" for petals on p. 226.

The reviewer, after using the book considerably in the field, can testify that this manual is one of the most satisfactory he has used. It is the result of years of painstaking, conscientious, competent work. Dr. Harrington has earned the thanks of all who work with plants in or near Colorado.

The book contains also a description of the Vegetation Zones of Colorado by David F. Costello. This consists largely of the listing of principal species in the various communities. The Plains Area is divided into 2 major communities, the Sand Sagebrush and the Mixed Prairie (considered as "short-grass disclimax").

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[1] Harrington, H. D. 1954. Manual of the plants of Colorado. x + 666 pp., 1 map. Denver: Sage Books. $8.00.

Vegetation and Watershed Management[1]

The subject with which Colman's book is concerned—the relation between vegetation and water yield—is strictly ecological. It is applied ecology not only in the sense that it concerns the influence of vegetation on water yield but also in its concern with the management of vegetation pointed toward the increase of both quantity and quality of water yielded.

The first 186 pages of the book are devoted to the presentation of background material, information largely already familiar to many ecologists.

For the ecologist perhaps the main contribution of the book starts on page 187. The remainder of the volume reviews research on various aspects of water yield and the vegetation cover of watersheds. Each of these chapters contains an organized presentation of the significant studies that have been made and concludes with an analysis of the present status of our knowledge of the subject. Almost invariably there is also the significant implication: this is what has been done; although it is valuable information much still needs to be done; here is the direction in which the research efforts should continue.

These particular chapters are entitled respectively: *"Alternative kinds of vegetation"*—in which comparisons are made between forest, pasture and various crops, most of them being concerned with the influence of vegetation on surface runoff and erosion, and which includes a section on soil freezing; *"Croplands"*—in which are reviewed studies in various parts of the United States and using various cultural methods, including strip cropping and rotation practices; *"Fire"*—in which seventeen pages are devoted to California and five to other sections of the country (an indication as to where the most obvious and severe effects of fire have been recognized as well as the part of the country where Colman has done most of his work); *"Grazed lands"*—in which is included the results of research on our western range lands and eastern pastures and one study in Switzerland; *"Tree-covered lands"* which includes effects of logging practices, evaporative losses of forests, soil permeability, the snow pack and riparian losses.

The book ends with a chapter on *"The opportunities and the challenge"* which serves the book in the same way that the concluding paragraphs serve the chapters. It includes a generalized appraisal of our present state of knowledge and emphasizes again the research needs. It concludes with a discussion of the problem of the application of research findings, a problem which is complex because it includes social, economic, and political factors in addition to physical and physiological ones.

"Vegetation and watershed management" is of especial value because of its synthesis of information on vegetation and water yield problems from a wide variety of sources and for its analysis of the problems and needs for further research.

The book was sponsored by the Conservation Foundation and represents one of a series of research studies on various aspects of the national water resource picture sponsored by that organization.

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[1] Colman, E. A. 1953. Vegetation and watershed management. xiii + 412 pp. illus. New York: The Ronald Press Co. $7.00.

Methods of Surveying and Measuring Vegetation[1]

This welcome addition to the literature brings together the methods and techniques which have been used and are being used in quantitative ecological studies of vegetation. It is divided into four parts: 1) In "Vegetation and its Sampling" vegetation terms are defined, the theory of sampling is discussed (in a separate chapter by G. M. Jolly) and sampling apparatus is reviewed. 2) In "Botanical Analysis" the criteria of frequency, number, area, and weight, are described clearly and with a useful discussion of methods applicable to each criterion. 3) Under "Productivity" detailed chapters discuss estimates and measurements of cover and weight, and the use of the animal as a measure of pasture production. These should make this section the most useful to those interested in methods of measuring yield and grazing-capacity of pasture and range land. 4) Finally, the problem of "Utilization" as this is affected by differences in grazing animals is discussed. Methods of determining utilization are briefly, but adequately, outlined. Most terms which would otherwise prove puzzling to many readers have been defined in the glossary at the end of the book.

The review classifies and compares methods used not only in purely botanical studies, but in all phases of pasture and range research. The extensive review of the literature, with the discussion of each surveying or measuring method, will greatly assist both the experienced worker and the newcomer into the field in selecting intelligently the method most suited to his problem. So many methods have been devised to suit particular purposes that most workers may find in this book a method suited to their problem, and so save the time generally necessary for the development of a new technique. The author indicates the importance of the statistical approach, and presents its more important phases in a form acceptable from the standpoint of the time and facilities available to most research workers. While the methods described are primarily applicable to grazing land, the book does provide a basis for approach by those interested in surveying land as yet untouched.

It would be well to point out here that while a tremendous array of techniques has been presented for use by ecologists, no mention is made of some of the most important pitfalls which could completely nullify the value of a survey. Plant species are discussed as though they are somehow intrinsically capable of defining the environment. The research pioneered by Clausen, Keck, and Hiesey has produced results of staggering importance to ecologists for they have found that the value of the species as an indicator of particular environmental conditions is dependent upon its degree of ecotypic development. This means that to produce biologically as well as statistically valid results, ecologists must be pre-

[1] Brown, Dorothy. 1954. Methods of Surveying and Measuring Vegetation. xv + 223 pp., 45 Figs. Bulletin 42, Commonwealth Bureau of Pastures and Field Crops, Hurley, Berks. Farnham Royal, Bucks, England. Commonwealth Agricultural Bureaux. 35s.

pared to undertake problems involving the taxonomy, cytology, genetics, and physiology of the plants and animals with which they deal.

The application of airphotos for the mapping of types and sub-types is given brief mention in the review. While it is a relatively new method, it has, when aided by a few pertinent field checks, proven to be vastly superior to ground surveys without the assistance of airphotos. Airphoto coverage is available for many areas of the world, and where it is neither available nor adequate, the cost of acquiring proper coverage will often be outweighted by the advantage of increased accuracy in type and sub-type mapping. Its greatest advantage in the near future is likely to be found in range studies of undeveloped areas, forested and non-forested. In regions where sufficient ground survey of vegetation types has been carried out and laboratory checks made, accurate maps which can sometimes indicate species of trees can be made with the aid of airphotos.

These criticisms are relatively minor for the book provides the first comprehensive review of vegetation survey and measurement techniques, and presents it in a fashion which can be readily understood even by the beginner.

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Dynamics of Growth Processes[1]

This book is continuous with the previous Growth Supplements which have recorded the collected symposium papers presented to the Society for the Study of Development and Growth. The present volume, which records the symposium under the same title held in 1952, initiates the new procedure to be adopted in the publication of these symposium reports. Both the volume and the new series will be generally welcomed by biologists. However, the purpose of symposia is to express and evaluate current thought. If the period of publication of the symposia in book form is to incur, permanently, a 2 year lag between presentation of the paper and its availability to the general reader one may well ask whether these volumes will really fulfill their proper function, for many of the contributions will have "gone cold" before they are read.

Thirteen chapters comprise the book. Almost all of these are admirably documented by references which direct the interested reader to the sources he may require. No short review can attempt to comprehend the range of material covered. The title "Dynamics of Growth Processes" merits comment. Few of the chapters treat growth dynamically in the sense that it is analyzed as a process proceeding through time. In the sense that they include material that relates to the motivating forces of growth all of the chapters are germane. The last four chapters in the book are, however, concerned with the over-all process of growth, with the criteria for determining the development of children (W. W. Greulich); the detection of rhythms in growth and the reconsideration of problems of relative growth or allometry (D. A. Sholl); the genetic control of growth (G. E. Dickerson); and the analysis of the growth of populations (F. E. Smith). By contrast, the first 4 chapters are concerned with the problems that underlie the growth process, such as the reduplication of protoplasmic units as seen in reproduction of viruses (L. M. Kozloff); amino acid (Novick and Szilard) and protein synthesis (A. W. Pollister), and the effect of the nucleus on the cytoplasm and on growth (G. Fankhauser). The remaining chapters deal with cell and tissue differentiation in animals (K. R. Porter), and plants (D. S. Van Fleet); physical (F. W. Went) and chemical factors (F. Skoog) that regulate growth in plants, and the chemical control over growth in animals (R. Gaunt).

To attempt to analyze any one of these chapters or refer to them in detail would require an arbitrary selection that would be inappropriate here. The impressive comment is, however, how rarely an author dealing with the fundamentals of growth and development ventures to say that any finality has been reached. The chapter on virus reproduction ends by posing the essential questions and by asking for more light on protein synthesis, the chapter on amino acid synthesis describes a novel system for its study in bacteria and the chapter on protein synthesis speaks of "most elaborately organized enzyme systems for the synthesis of a protein molecule" in microsomes "of extreme heterogeneity." There is challenge, but little comfort and no certainty here.

Despite much work, those who attempt to see tissue differentiation, especially in plants, in terms of the enzymes in the differentiating cells have available an odd collection of facts ranging from an observation that urease is synthesized in the meristem but was not present in cambium or its derivatives. Since we do not know whether urease plays any part in the jack bean from which it is commonly isolated, this fact is of dubious value. It is one thing to determine the presence of an enzyme *in situ* by microchemical test—it is another to show that its presence there has any significance in the causation of growth or differentiation.

F. W. Went makes out the case for the regulatory importance of physical factors in the control of growth and development and sees diffusion, operating in the transfer of growth substances and anti-metabolites as an essential part of the machinery of growth. In the ensuing chapter Skoog dwells on the chemical machinery of growth in plants and summarizes a large amount of data obtained by tissue culture methods and by the experimental control of development. The trail of auxin (indole acetic acid) is traced through "each phase of the development of higher plants, so that its domain now covers almost anything from the general increase in size of cells to the differentiation of all organs." Even the author admits that "it is difficult to see, even granting unusual versatility to a single substance, how in all these cases its effect could be a primary one" so that some mysterious "master reaction" is posed which apparently lies in the domain of interaction between nucleic acids and I.A.A. which would "presumably lead to corresponding changes in cytoplasmic protein composition." And so it goes.

The Dynamics of Growth Processes solves few problems, though it poses many for those who will ponder these things. It furnishes the modern glossary through which to implement the ancient injunction to "consider the lilies of the field, how they grow."

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[1] Boell, E. J. (ed.). 1954. Dynamics of Growth Processes. vii + 304 pp., Illus. Princeton: Princeton University Press. $7.50.

Agricultural Geography of the World[1]

Dr. Papadakis has made an ambitious attempt in this short, concise, well-written, and well-illustrated volume to present an agronomist's view of world agricultural regions. Because of its brevity, and because the author has succeeded so well in presenting in abridged form all of the principal elements that go into a definition of an agricultural region, this, in this reviewer's opinion, deserves to become a standard text in the fields of geography, agronomy, and crop ecology.

Dr. Papadakis states that his classification of agricultural climates is based on four elements: winter hardiness, summer heat and duration of summer, annual hydric index, and seasonal distribution of the hydric index. The first of these, winter hardiness, is determined by using three principal crops: winter wheat, winter oats, and citrus crops, and establishing two additional categories, i.e. completely frostless and with a mean annual minimum temperature above 59° F. Summer heat and duration is also based on three crops: wheat, maize, and cotton. The annual hydric index, determined by dividing the mean annual rainfall by the sum of mensual water needs (related to transpiration, soil evaporation, and the saturation deficit) serves as a third principal element of agro-climatic regions. This annual hydric index ranges from "polyhygrophytic" (annual humidity coefficient greater than 2.64) to desertic. Finally, the seasonal distribution of the hydric index is defined as falling into one of three categories: mediterranean, or winter rain type, isohygrous type with fairly equal distribution, and monsoon type with summer rainfall predominant. Subsequent to this general discussion of his climatic classification scheme, the author discusses growth rate and growth rhythm, and soil types as determinants of vegetation associations.

The second half of the book is devoted to a brief discussion of the agricultural regions of the world, determined on the basis of the classification described above, and shown on the accompanying world map. For each of the agricultural regions the author gives a brief description of its climate, principal crops, types of soil, types of native vegetation, annual growth index, and growth rhythm. Ninety-eight regions are thus described.

While the general principles of the classification scheme can be readily discerned, the author's coverage here becomes rather spotty, and is characterized by very great detail in some parts of the world (e.g. southeastern South America) and lack of adequate discussion in others (e.g. eastern Africa). In this reviewer's opinion, however, such a variation of coverage does not detract from the value of the book, rather, it would seem to stimulate further, detailed research that would permit better agro-geographical knowledge of the world.

The world maps appended to "Agricultural Geography of the World" illustrate, besides the agricultural regions established by the author, zonal vegetation types, zonal soils, and vegetal growth and rhythm. In addition, there are three plates of diagrams, showing annual growth indices, thermo-diagrams, and annual hydric indices for selected places throughout the world.

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[1] Papadakis, J. 1952. Agricultural Geography of the World. (Climate, Growth Rate and Rhythm, Vegetation, Soils, Crops, Agricultural Regions). Buenos Aires: published by the author. x + 131 pp., 3 plates of diagrams, 4 plates of world maps.

Conservation of Natural Resources[1]

Conservation has been a central topic of discussion in American public affairs for well over half a century. Beginning with Marsh, Powell, and Shaler, and the men who may well be considered the founders of the American conservation movement, Theodore Roosevelt, Gifford Pinchot, and their contemporaries, the preservation of our heritage has been the constant subject of public debate, legislation, and practical policy. "Conservation of Natural Resources," ably edited by Professor Guy-Harold Smith, provides a detailed and well-presented survey of the subject.

Twenty-one authors have contributed to this volume, which has thus become a handy compendium of the many facets of resource conservation and management. An historical introduction of the development of the idea of conservation in America is followed by a series of chapters grouped according to main topic headings: conservation of the soil in its various aspects; conservation of forests; management of water resources; conservation of economic minerals; wildlife conservation; conservation and its relation to recreational development; and the role of planning in conservation.

It is almost inevitable that a volume of such encyclopedic scope will present a wide variety of interpretations of the term "conservation." One might, perhaps, wonder why demography, under the title "Conservation of Man," would be part of such a survey, since, to this reviewer at least, this implies an unnecessary extension of the definition of "conservation." On the other hand, such chapters as Professor Wolfanger's "The Great Soil Groups and Their Utilization," the late Professor Ralph Brown's "American Irrigation," and Professor Smith's "Floods and Flood Control," may well be considered as models of concise yet comprehensive coverage of these essential aspects of resource conservation.

An interesting reflection on the rapidly changing outlook in certain fields of conservation is provided by the chapter on "Water Supply for Domestic and Industrial Uses," where less than a third of the space utilized is devoted to the problem of water conservation. Pollution by industrial users and the vast increase in domestic and industrial water consumption due to such new developments as air conditioning and the spread of suburban housing developments has brought water conservation to the fore as one of the most critical aspects of resource management in the United States.

One minor criticism of the scope and organization of "Conservation of Natural Resources" might be made by pointing out that the title of this volume ought to include the qualifying addition "in the United States," since precious little is said of the lack or presence of conservation policies in other parts of the world. This is a topic

[1] Smith, Guy-Harold (Editor), 1950. Conservation of Natural Resources. 552 pp. New York: J. Wiley and Sons. $6.00.

that is well deserving of at least cursory treatment at a time when agencies of our government and private foundations are actively engaged in conservation projects all over the world.

A most valuable feature of this volume is its body of illustrations, both maps and photographs. These, as well as selective bibliographies at the end of each chapter, make this an excellent choice for teaching and general reference purposes.

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